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THE UNIVERSITY OF ALBERTA

THE EFFECT OF BYPASS PROTEIN SUPPLEMENTATION ON THE ENERGETIC EFFICIENCY OF LAMBS IN COLD AND WARM ENVIRONMENTS

By

Gesa Erica Margarete Graefin von Keyserlingk

A thesis submitted to the
Faculty of Graduate Studies and Research in partial
fulfillment of the requirements for the degree of
Master of Science.

IN

ANIMAL NUTRITION

DEPARTMENT OF ANIMAL SCIENCE

EDMONTON, ALBERTA

SPRING, 1992

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ISBN 0-315-73135-4

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DEGREE: Master of Science

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled THE EFFECT OF BYPPASS PROTEIN ON THE ENERGETIC EFFICIENCY OF LAMBS IN COLD AND WARM ENVIRONMENTS submitted by GESA ERICA MARGARETE GRAEFIN VON KEYSERLINGK in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in ANIMAL NUTRITION.

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Date April 22, 1992

DEDICATION

To my parents

Ingeborg and Alexander von Keyserlingk

ABSTRACT

Forty-eight crossbred lambs (22.5 kg ± 2.6 kg) of equal numbers from both sexes were used to observe the effect of protein supplementation (canola meal or fishmeal) and temperature (21 ± 1.8°C or 4.7 ± 1.7°C) on growth and energetic efficiency in a 2 x 3 x 2 factorial experiment. Twelve lambs were slaughtered at the onset of the trial to determine initial composition. The remaining 36 were fed diets consisting of 50% concentrate and 50% straw at 78 and 83 $g/kg^{.75}$ daily in the warm and cold, respectively, for an 85 day period. Calorimetry-balance and comparative slaughter techniques were both used to estimate energy retention. Apparent digestibilities of dry matter, gross energy and organic matter were decreased ($P<.05$) in response to the cold. Methane production was not affected by temperature. When adjusted to equal dry matter intakes, daily heat production was decreased ($P<.05$) with cold exposure (173 vs 186 $kcal/kg^{.75}$) in response to the lower metabolizable energy intakes (194 vs 213 $kcal/kg^{.75}$). Cold-treated lambs retained less total energy ($P<.01$) as well as less ($P<.05$) fat and protein energy. Protein supplementation increased ($P<.05$) digestibility of nitrogen while fishmeal supplementation decreased fibre digestibility. Daily gains of the control, canola and fishmeal supplemented lambs were 81, 91 and 101 $g/kg^{.75}$, respectively, however protein supplementation did not affect efficiency of live weight gain. Supplementation with protein increased ($P=.06$) energy retained as protein, estimated by comparative slaughter, however it did not affect total energy retained ($P>.10$) or energetic efficiency. Energy retention estimated from the calorimetry-balance technique was 30-70% greater than that estimated from the comparative

slaughter technique. It was concluded that methane production in lambs with fleece was not decreased when the temperature was dropped from 21 to 5°C and that energetic efficiency was not affected by the concentration of protein in the diet. Additionally, the comparative slaughter technique was a more precise method of estimating energy retention than the calorimetry technique.

ACKNOWLEDGEMENTS

I would like to express my sincere thanks to my supervisor, Dr. G. W. Mathison for his time and immeasureable patience. His support and faith in my ability were the best encouragement any student could hope for. I would also like to thank Dr. J. R. Thompson for his encouragement and understanding when times were tough and for companionship in the innumerable trips to "Java Jive". As well, the help from the staff at the Metabolic Unit, the lab and the summer students was irreplaceable and greatly appreciated. In particular Jack Francis for his help during the course of the animal trial and Irena Vlach for her assistance with the heat production calculations.

Numerous discussions with my fellow graduate students were priceless for their insight, with respect to my research and for the reassurance that I was not alone in making blunders. With respect to my parents, my sisters, Marina and Tinka, and my cousin, Mechthild Borsch, I can only say that your phone calls were always timely and greatly appreciated. I couldn't have done it without you.

I would like to extend my appreciation to Dr. M. A. Price, Chair of the department of Animal Science, who made departmental facilities available for my studies, and the National Sciences and Engineering Research Council and the Alberta Agricultural Research Institute for their financial assistance.

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I. LITERATURE REVIEW

Bypass protein is dietary protein which will escape degradation in the rumen, however, is available for absorption in the small intestine. Bypass protein is also known as escape or rumen undegradable protein (UDP). Bypass protein will result in increased voluntary intake (Gill et al., 1987; Brand et al., 1991), daily gains (Klopfenstein et al., 1982) and feed efficiencies (Hennessy and Williamson, 1990; Petit et al., 1991) in ruminants eating low quality forages. These results, however, have not always been consistent (Yilala and Bryant, 1985). The mechanisms for the production responses are as yet not known, however, it has been suggested that bypass protein supplementation will improve the efficiency of metabolizable energy (ME) utilization (Ortigues et al., 1990; Hennessy and Williamson, 1990). There is, however, limited information on this response therefore there is a need for further research in this area.

Differences in the responses of animals to bypass protein supplementation have been observed, with animals in the tropics responding more consistently than those in more temperate climates (Leng, 1989). There is, however, little information on a possible diet by temperature interaction on energetic efficiency.

1.1 The Effect of Bypass Protein

1.1.1 Effect of Bypass Protein on Intake, Growth and Feed Efficiency

There have been numerous experiments in which bypass protein supplementation has resulted in increases in voluntary intake (Ørskov et

al., 1973; Veira et al., 1985; Yilala and Bryant, 1985; Coombe, 1985; Seoane et al., 1990; Brand et al., 1991), live weight gains (Yilala and Bryant, 1985; England and Gill, 1985; Veira et al., 1988; Anderson et al., 1988) and improved feed efficiency (Ørskov et al., 1974; Veira et al. 1985, 1988; Hennessy and Williamson, 1990; Petit et al., 1991). Since observing the effect of bypass protein on intake was a primary objective of a number of these trials, many were conducted at *ad libitum* intake thereby making it difficult to distinguish between responses brought about by the increased intake from responses brought about by changes in animal efficiency. In addition, a number of trials have been performed without a degradable protein source as a control treatment, hence it is impossible to determine whether the animal responses observed were the result of the bypass protein or simply protein supplementation.

1.1.1.1 Bypass Protein Supplementation at Ad libitum Intake. Yilala and Bryant (1985) reported that supplementation with protected rapeseed meal increased daily gains in lambs fed a basal diet of silage, however voluntary intake was also significantly increased when crude protein levels were increased from 11.5 to 15 and 17%. No differences were detected between lambs fed untreated or formaldehyde treated (bypass treatment) rapeseed meal. In a study by Veira et al. (1985) substantial reductions in the amount of feed required per kilogram of gain were reported when fishmeal was offered with grass silage, but again voluntary intake of silage was increased making it difficult to differentiate between intake responses and responses to bypass protein supplementation. Veira et al. (1990) observed that live weight gains were increased by 15% when fishmeal replaced soybean meal in grass silage diets, however, this

increase was proportional to the greater nitrogen intake of the fishmeal supplemented animals. In an experiment where increasing levels of fishmeal did not increase intake (Gill et al., 1987), live weight gain of cattle did increase. This suggests that the growth of the cattle on the control diet (silage) was limited by protein, however it does not indicate whether the response in live weight gain was due to the bypass protein or whether this protein deficiency could have been alleviated with a more degradable source of protein. Steen (1985, 1988) was unable to detect any response in performance of cattle when fishmeal was added to silage-based diets but did observe an increase in live weight gain in a similar subsequent trial (Steen, 1989). In this trial, however, there were no differences in live weight gains between rumen undegradable protein (UDP) and rumen degradable protein (RDP) supplemented silage-based diets. Results from Nebraska, have demonstrated increases in average daily gains in growing steers when an escape protein replaced soybean meal (Klopfenstein et al., 1982).

Similar results are found with concentrate-based diets. Petit et al. (1991) reported no increase in live weight gains when veal calves were offered a diet of whole shelled corn grain supplemented with either soybean meal or fishmeal at a crude protein level of 16%. They did, however, observe a decrease of .13 units in the feed to gain ratio in the fishmeal supplemented calves due to a slight decrease in their feed intake. These results are supported by Thonney and Hogue (1986) who reported a similar insignificant response when cottonseed meal replaced soybean meal, also in corn-based diets.

Results with low-quality forages have also been variable. In an

experiment performed by Coombe (1985), formaldehyde treatment of solvent extracted rapeseed meal and sunflower meal increased intake by 44 and 50% respectively over that of mature sheep fed the basal diet of 80% oat straw supplemented with urea. Live weight gains were also increased from 30 to 168 and from 30 to 157 g per day respectively when rapeseed meal and sunflower meal replaced urea in sheep suggesting that the protein supply was insufficient but giving no indication if UDP was essential. Hennessy and Williamson (1990) detected an improvement in feed to gain ratios which decreased from 15 to 8 kg per kg of live weight change when protected casein was substituted for urea in diets based on low quality hay containing 10% crude protein. However, in this case the response was brought about by a significant increase in live weight while voluntary intake remained the same.

Although changes in live weight gain and feed efficiency have been observed in a number of trials in which a bypass protein was used, it is difficult to interpret the results due to the differences in nitrogen intake. If animals are receiving diets with insufficient levels of protein, an increase in protein intake is expected to result in greater intakes as well as live weight gains, which was the case in a number of the previously mentioned trials.

1.1.1.2 Effects of Bypass Protein at Restricted Levels of Intake. Increases in live-weight gains and feed to gain ratio have also been observed in a number of trials in which cattle were fed bypass protein-supplemented diets at restricted levels of intake (Smith et al., 1985; Ortigues et al., 1989, 1990), thereby removing the confounding factor of differences in voluntary intake. However interpretation of these studies

is still difficult due to other confounding factors such as differences in protein type and quantity.

In an experiment designed to test the hypothesis that fishmeal supplementation increased the efficiency of nutrient use, dairy heifers were fed a basal diet of ammoniated straw and sugarbeet pulp, supplemented with increasing levels of fishmeal (Oldham and Smith, 1981). Protein supplements that largely escaped rumen degradation consistently supported higher weight gains than other, more degradable supplements. Smith et al. (1985) confirmed these results in a later experiment where liveweight gains in yearling dairy heifers were reported to have increased from 269 to 455, 327 and 358 g/day when urea was replaced by fishmeal, protected soya-bean meal or unprotected soy-bean meal respectively. Ortigues et al. (1989) found that replacement of barley with fishmeal increased live-weight gains by 43% in dairy heifers fed a basal diet of ammoniated straw and barley. This response can be attributed to the effect of fishmeal as a protein supplement however it gives no indication as to fishmeal's value as an escape (bypass) protein. In a similar experiment (Ortigues et al., 1990) in which two increments of fishmeal were added to the basal diet of straw and sugarbeet pulp, an increase in live weight gain was observed in the fishmeal-supplemented diet over that of the control, but again, the control contained only 9% crude protein whereas the two diets containing fishmeal contained 12 and 16% crude protein.

As previously observed it is difficult to evaluate the potential benefits of bypass protein due to the variations in basal diets, and in the types and quantities of protein supplied. Despite these difficulties, improvements in live weight gain have been detected which are not

explained by differences in intake. There is, therefore, a need to determine the mechanism responsible for the improvements in growth rate and efficiency of ruminants fed bypass protein.

1.1.2 Digestibility

A possible potentiator of the above results may be found in changes in the digestibility of diets supplemented with different protein regimes. The effects of bypass protein on fibre digestibility have generally been positive. Hussein et al. (1991) reported that in forage:concentrate diets (1:1.5) fishmeal increased ruminal digestion of neutral detergent fibre (NDF), and acid detergent fibre (ADF) by 89 and 74% respectively when it replaced soybean meal. Increases in fibre digestion were also observed when a protein source (fishmeal) replaced a non-protein source (urea) of nitrogen (Oldham and Smith, 1985; McCallan and Griffin, 1987). McCallan and Griffin (1987) found a 12% increase in mouth to abomasum cellulose digestibility in steers supplemented with fishmeal compared with those supplemented with soybean meal. Cecava et al. (1991) observed a 12% increase in total tract digestion of NDF in steers fed a corn gluten meal and blood meal mixture (a bypass protein) versus soybean meal however McCarthy et al. (1989) and Brand et al. (1991) observed no effect of bypass protein supplementation on fibre digestion.

The effects of a supplement high in rumen undegradable protein (UDP) on organic matter digestion have been more variable. In various trials in which a diet supplemented with either a UDP or rumen degradable protein (RDP) source was fed to sheep or steers, the site and extent of organic matter digestion remained unchanged with a variety of basal diets,

including forage-concentrate diets of differing ratios (Ortigues et al., 1990; Hussein et al., 1991; Cecava et al., 1991), grass silage (Cottrill et al., 1982) and concentrate (Ørskov et al., 1974; McCarthy et al., 1989). England and Gill (1985), however, found a 3.6% increase in organic matter digestibility in cattle when fishmeal was added to the basal diet of grass silage. Brand et al. (1991) found a 13% increase in organic matter digestibility in wheat-straw diets with the inclusion of fishmeal.

Hussein et al. (1991) suggested that, since the protein from fishmeal is digested at a slower rate than soybean meal, the supply of nitrogen, essential factor for microbial growth, may be available for a longer period of time after feeding when fishmeal is fed. This could have a significant effect on rumen fermentation when feeding low quality forages where digestibility can be a factor limiting nutrient utilization.

1.1.3 Protein Flow in the Rumen and Small Intestine

The natural flow of nutrients supplied to the intestine may be inadequate for rapid growth (Owens and Zinn, 1988), thus there is potential for manipulating this flow to optimize nutrient supply to improve production responses. The nutrients which have been emphasized the most in beef and sheep production with reference to intestinal flow have been amino acids. There are three major sources of amino acids entering the small intestine: microbial protein, dietary amino acids escaping ruminal degradation (bypass), and endogenous protein. Since the effect of dietary manipulation on this latter source is difficult to measure, it is the first two supplies which have received the most attention. The amino acid requirements of the tissues increase with

increasing levels of production and, although the requirement for undegradable or bypass protein also increases (Hussein and Jordan, 1991), microbial protein synthesis is still a key supplier of nitrogen to the small intestine.

1.1.4 Flow of Dietary and Microbial Nitrogen to the Small Intestine

Various workers have found that total nitrogen flow to the duodenum remains unchanged whether RDP or UDP supplements are added to the diets (Mercer et al., 1980; Lindberg, 1985; McCarthy et al., 1989; Willms et al., 1991), while others (Titgemeyer et al., 1989; Hussein et al., 1991; Cecava et al., 1991) have reported increases in total N flow to the duodenum. Cecava et al. (1991) reported a 14% increase in total nitrogen flow when a corn gluten meal and blood meal mixture replaced soybean meal. However, with this increase in total flow, a concomitant decrease in microbial flow has been observed with some escape proteins (Hussein et al., 1991; Titgemeyer et al., 1989; McCarthy et al., 1991; Cecava et al., 1991). This greater passage of microbial protein to the duodenum with soybean meal may be accounted for in part by the increased efficiency of microbial protein synthesis (Cecava et al., 1991).

McCarthy et al. (1989) found no significant differences in the passage of amino acids to the duodenum when RDP supplements replaced UDP supplements and suggested that microbial fermentation may have an equalizing effect on the amino acid composition of digesta. In contrast, other workers have found differences in the amino acid composition of digesta in animals fed different supplements (Mercer et al., 1980; Hussein et al., 1991; Titgemeyer et al., 1989). In a comparison of groundnut

meal and fishmeal, Mercer et al. (1980) found that fishmeal provided greater amounts of methionine, lysine, threonine and alanine, and smaller amounts of glutamic acid, cysteine and arginine than groundnut meal to the small intestine. Gill and Beever (1982) found that, not only did fishmeal increase total amino acid flow by 34%, but the balance of amino acids entering the duodenum was also improved. Fishmeal supplementation of lambs consuming a basal diet of barley resulted in a 16% greater absorption of total amino acids, essential amino acids and non-essential amino acids, than soybean meal supplementation of the basal diet (Hussein et al., 1991) even though total duodenal amino acid flows remained the same. This increase was attributed to the higher-quality dietary protein from fishmeal which entered the small intestine.

Although distinct differences in the amino acid profile of duodenal digesta from steers fed different diets have been reported, the pattern of non-bacterial amino acid reaching the duodenum generally reflects the amino acid pattern of the protein source (Redman et al., 1980; Titgemeyer et al., 1989) hence, the source of bypass protein chosen for supplementation should complement the amino acid profile of the basal diet. In addition, although the flow of microbial protein may decrease with the inclusion of bypass protein, the flow of dietary protein appears to increase. These results suggest that escape proteins can be used efficiently in manipulating amino acid flow to the small intestine in the ruminant animal. The increased amino acid flow could result in improvements in the energetic efficiency of the animal (as will be discussed later).

1.1.5 Efficiency of Microbial Protein Synthesis

Lindberg (1983) observed a 53% decrease in efficiency of microbial protein synthesis when fishmeal was substituted for rapeseed meal in a hay and barley based diet, however these differences were not significant. Significantly lower bacterial efficiencies for sheep (Mercer et al., 1980; Hussein et al., 1991) and cattle (Cecava et al., 1991) have been observed when fishmeal was added to the diet. Cecava et al. (1991) suggests consideration of NH_3-N as a potential effector of these results since NH_3 is required for bacterial growth (Satter and Slyter, 1974). However, although NH_3-N may play a significant role in microbial protein synthesis, other nutritional factors such as availability of peptides, amino acids or other nutrients (Cecava et al., 1991) may also be important. Hussein et al. (1991) and McCarthy et al. (1989) both reported concomitant decreases in NH_3-N with lower efficiencies of bacterial synthesis when UDP replaced RDP in the diets, however in both cases NH_3 should not have limited microbial activity according to information of Satter and Slyter (1974), hence other factors as mentioned above may have limited microbial synthesis.

In contrast to the findings of the previous workers, Cottrill et al. (1982) observed an increase in bacterial efficiency when fishmeal replaced urea in four isonitrogenous supplements containing urea-N and fishmeal-N in the following proportions; 3:1, 1.4:1, 0.6:1 and 0.3:1 when steers were fed a basal diet of maize silage and barley. These four diets were such that fishmeal provided approximately 13, 23, 32 and 45% of the total nitrogen content of the diets. The increase in bacterial efficiency was, however, observed only in the first two increments and not in the

third. The highest inclusion of fishmeal resulted in a decline in efficiency of microbial protein synthesis. Cottrill et al. (1982) suggested that a lack of rumen degradable protein in the third increment may have caused this depression in efficiency of microbial synthesis. Dawson et al. (1988) reported a 53% increase in efficiency of microbial protein synthesis with the addition of fishmeal to silage diets in steers, however nitrogen intake per day was also increased by 48% indicating that the control animals may have had insufficient degradable protein to support optimal microbial growth. Other workers (Redman et al., 1980; Willms et al., 1991) found no differences in efficiency of bacterial CP synthesis when a UDP supplement replaced a RDP supplement.

No consistent effects of bypass protein on efficiency of microbial synthesis are apparent in the literature at this time. However, the few effects observed have been negative and therefore cannot be the source of improvement in animal performance when bypass protein is fed.

1.1.6 Effect of Bypass Protein on the Efficiency of Metabolizable Energy Utilization

It has been suggested that the efficiency of ME utilization could be changed by manipulating dietary protein quantity (Walker and Norton, 1971; Blaxter and Boyne, 1978) and type (Leng, 1989; Hennessy and Williamson, 1990; Ortigues et al., 1990). Bypass protein has thus been implicated as a possible tool in manipulating the efficiency of ME utilization. The mechanisms, to date, are not fully understood, however, it is believed that utilization of amino acids post-ruminally eliminates energy losses associated with fermentation as well as losses incurred in

the transformation of dietary protein to microbial protein (Chalupa, 1974) and hence may contribute to improved production.

In a trial conducted by Veira et al. (1988), it was suggested that the effect of fishmeal on growth rate of steers fed a basal diet of grass silage may have been a result of an improved protein to energy ratio in the end products of digestion which allowed the younger growing cattle to meet their potential for protein deposition. Results from Oldham and Smith (1981) showed increased rate of gain at a constant digestible organic matter intake with protein supplementation. Ortigues et al. (1989) suggests that this implies that protein supplementation increased efficiency of nutrient use. In further work of Ortigues et al. (1990), two levels of fishmeal were given to dairy heifers. They hypothesized that an increase in efficiency would be measured in the first increment of fishmeal (76 g fishmeal/kg DM of basal diet) as a result of a reduction in wasteful oxidation of acetate and enhanced tissue deposition, while no response would occur with the second increment (152 g fishmeal/kg DM) if maximum protein deposition had already been reached. This response did occur however, some caution must be used in interpretation of the data due to the large between-animal variability. Hennessy and Williamson (1990) also suggested that the lower feed conversion ratio of cattle supplemented with formaldehyde treated casein indicated a greater efficiency of ME use for gain than would have occurred in cattle supplemented with urea. Hennessy et al. (1990) postulated that the increase in efficiency was due to the increased availability of protein for digestion in the intestine and in addition, an improved balance of essential amino acids may have been a factor.

Walker and Norton (1971) observed differences in efficiencies of ME use in young lambs who were provided with one of three diets which contained the same ME content but with varying protein content. They found that lambs fed a diet with 26% protein had significantly greater efficiencies of ME use than those fed diets containing either 10 or 46% crude protein. In an analysis of 79 experiments, Blaxter and Boyne (1978) found that energy retention was not directly proportional to the amount of ME supplied, but that it varied with the metabolizability of the mixture, and also with the fibre and protein content of the diet.

Although results from attempts to manipulate the efficiency of ME utilization in ruminants through manipulations of dietary protein have not been unequivocal (Ortigues et al., 1990), the positive responses first reported by Walker and Norton (1971) and Blaxter and Boyne (1978) and later by other workers (Ortigues et al., 1990) are encouraging. These results have demonstrated the potential for obtaining additional growth at a set ME intake from a non-rumen degradable protein supplement without modification of the basal forage in the diet (Hennessy and Williamson, 1990). There is, however, a need for a comparison of the efficiencies of ME utilization of forage diets supplemented with a bypass protein and those supplemented with a more degradable source of protein, since improvements in efficiencies have been observed primarily when an escape protein replaces the non-protein nitrogen source of urea. In addition, the mechanisms which may change the efficiencies of ME use with increasing protein also need to be examined.

1.2 Heat Production

1.2.1 The Heat Increment of Feeding

In the ruminant the major components of the heat increment of feeding (HIF) include the energy cost of eating and ruminating, the heat of fermentation, the work of digestion and inefficiencies in nutrient metabolism. Changes in one or several of the components of the HIF may lead to a subsequent change in efficiency of ME utilization. There is a great deal of transformation and synthesis of nutrients and metabolites through the microbial pool in ruminants compared to their monogastric counterparts, who will derive many of these nutrients directly from the diet. Hence it is particularly difficult to quantify the components of the HIF and to predict energetic responses to changes in nutrient intake in ruminant animals (MacCrae and Lobley, 1986). Despite this, researchers have attempted to estimate the relative energy costs of the components of the HIF.

1.2.1.1 Energy Cost of Eating and Ruminating. Osuji et al. (1975) demonstrated that the energy cost of eating for sheep was seven times greater when chopped dried grass was fed than when pelleted dried grass was fed and suggested that the total energy cost of eating is related to the time taken to eat. In a comparison of sheep fed orally or with a rumen fistula, Osuji et al. (1975) observed that the increase in heat production when a sheep was fistula-fed was only 2-8% of the increase when the animal was fed orally thus indicating that most of the increase in heat production during eating was due to the energy cost of eating rather than to the energy cost of digestion and metabolism. There was, however, only one animal used in this experiment. Since less time is required to

eat pelleted rations than non-pelleted forages, Webster (1980) estimated that although the total ME cost of eating for sheep grazing at a maintenance level of intake would be 3% of its total heat production, the energy cost of sheep eating a maintenance ration which was pelleted would be negligible. This supports earlier observations by Osuji et al.'s (1975) that time spent eating may be directly related to the total energy cost of eating.

Balch (1971) reported that on average, rumination time was twice that of eating time thus it was surprising when rumination energy costs were estimated to be only about 10-20% of total eating costs (Webster, 1980). A notable difference observed between these two activities has been in the distribution of blood flow; decreases in plasma volume at the onset of eating have been measured by Christopherson and Webster (1972) whereas such changes have not been observed during rumination. Webster (1980) suggests that the extra energy cost associated with eating in comparison to rumination may be related to this redistribution of blood.

1.2.1.2 Heat of Fermentation. Baldwin et al. (1970) estimated that the total loss of feed energy to fermentation does not exceed 6.4% of the digestible energy irrespective of the nature of the feed. This is supported by Webster et al. (1975) who showed that the energy expended by the gut was the same for both pelleted or chopped dried grass. *In vitro* measurements from sheep (Marston, 1948) and cattle (Houpt, 1968) have indicated that the heat of fermentation is slightly greater (6-8% of fermented energy) than the values calculated by Baldwin (1970). Webster's (1980) *in vitro* measurements are in agreement with this and lend credence to Hungate's (1966 cited by Webster, 1980) suggestion that the heat of

fermentation in ruminants is relatively constant.

1.2.1.3 Work of Digestion. In contrast to Wester et al.'s (1975) observations that there were no differences in the energy use by gut tissue in steers fed either pelleted or dried grass, Lobley (1986) reported that the work associated with digestion is higher with more fibrous forages. Huntington et al. (1988) reported the oxygen consumption of portal drained viscera was 23 and 29% of total oxygen consumption for steers fed alfalfa and orchardgrass, respectively, at high intakes. This effect is believed to be because the consumption of more fibrous feeds is associated with increased secretion of saliva and digestive fluids, as well as potentially greater desquamation through physical action which may result in this greater energy cost of digestion (Lobley, 1986).

1.2.1.4 Nutrient Metabolism. The cost of metabolism depends, to a certain extent, on the amount of transformation that the nutrient is subjected to while it is being utilized by the body (Milligan, 1971). The relative values of several nutrients for maintenance in comparison to stearate were investigated using sheep in negative energy balance (Baldwin, 1980) and it was found that glucose, acetate and propionate had relative values of 105, 89 and 91% respectively. Thus energy expenditure at maintenance may vary significantly depending upon the energy source (Baldwin, 1980). Similar variations in efficiencies have been estimated for gain. For example, glucose can be converted to lactose much more efficiently than propionate can, hence ruminants have a greater cost for milk synthesis than monogastrics do (Baldwin, 1980).

Energetic inefficiencies are also involved in nutrient storage. Milligan (1971) estimated that the storage of acetate as lipid before it

is used for ATP generation would result in a 19% loss of the total available energy from acetate. A similar calculation was made by Baldwin (1980), who estimated that energy costs of nutrient metabolism could be increased from 15.4 to 27.6% if fatty acids were used for maintenance functions instead of volatile fatty acids (VFA), and if the VFA's were stored as fat in the place of fatty acids.

An important component of nutrient metabolism is tissue accretion. Early theoretical estimates of the efficiency of ME utilization for protein and fat synthesis indicated figures of approximately 90% and 70% respectively (Blaxter 1962). This was later challenged by various workers (Ørskov and MacDonald, 1970; Rattray et al., 1974; Graham, 1980) who found that protein deposition in growing animals was energetically less efficient than previously believed. Old and Garrett (1985) estimated the efficiencies of energy utilization to be 49 to 58% and 10 to 11% for fat and protein deposition, respectively, in finishing steers. More recent estimations of efficiencies of ME use for tissue growth in steers, also obtained using multiple regression analysis, have been 71 to 91% for fat and 11 to 13% for protein (Delfino and Mathison, 1991) in steers. Reeds and Fuller (1983) reviewed results which demonstrated that whole-body protein synthesis occurred at twice the rate of protein deposition. Thus, it is likely that the low estimates of efficiencies of protein synthesis are the result of the cost associated with protein turnover as suggested by Garrett and Johnson (1983). In contrast to protein it is believed that fat acts as a reserve with a slow turnover rate hence the efficiency of ME use for fat deposition in ruminants is in all cases much greater than that for protein (Geay, 1984).

In addition to the cost of protein turnover, a large proportion of the heat increment of feeding has been assigned to ion transport and a smaller proportion substrate cycling (Summers et al., 1988).

Although estimates such as those of Baldwin (1980) are only theoretical, they do give an idea to the extent to which nutrient metabolism can affect the heat increment of feeding and thus the efficiency of ME utilization. Some of these factors are discussed in more detail below.

1.2.2 Factors Affecting Energetic Efficiency

1.2.2.1 *Protein Turnover.* Reid et al. (1980) reviewed results which demonstrated that the energetic efficiency was greater in animals which deposited more body energy as fat than protein, implying that ME is utilized more efficiently in the net synthesis of fat than in the net synthesis of protein. The lower efficiency of use associated with protein deposition is most likely the result of the costs associated with protein turnover as well as the transport of contributing nutrients and ions (Garrett and Johnson, 1984). This turnover is, however, only partly related to growth, with the replacement of enzymes involved in digestion and metabolism (Webster, 1980), cellular protein turnover (Reeds and Fuller, 1983) and intracellular protein (Milligan and Summers, 1986) also being involved.

The rate of protein synthesis and degradation appears to be dependent on a number of factors such as nutrient intake, age, thermal stress, lactation and gestation however only the effects of age and nutrient intake will be discussed in this review. Although protein

synthesis and breakdown continue throughout life, the rate at which they occur varies with age. This was demonstrated by Reeds et al. (1980) who found that as animals grew larger, there was a significant increase in total protein synthesis. However, expressed as g $N/kg^{.75}$ per day, protein synthesis falls in older animals whereas the rate of protein breakdown does not change significantly (Reeds et al., 1980). It is possible that the response of protein synthesis to different nutrient deficiencies varies with age. Golden et al. (1977a, 1977b) suggested that protein synthesis in malnourished children did not respond to changes in protein intake, however an increase in protein synthesis was measured when energy intake was increased. Garlick (1973 cited by Reeds et al., 1980), however, found that the reverse was true for adults. Although the differences may be due to age, it is also possible that the magnitude of the changes may be dependent on the basal levels of protein and energy to which the supplement is added (Reeds et al., 1980); the relationship between protein intake and synthesis may become uncoupled at low levels of intake.

Reeds and Fuller (1983) summarized findings and derived a positive linear relationship between intake and both protein synthesis and degradation for combined protein and energy intakes ranging from fasting to three times maintenance. This relationship was derived from experiments involving pigs, rats and humans. Lobley et al. (1987) reported a similar relationship for cattle. Protein synthesis appeared to increase with increasing intake at a greater rate than did protein degradation therefore it was surmised that quantitatively, protein synthesis was the most important factor controlling N retention (Reeds

and Fuller, 1983).

Although there is little information on the effect of protein synthesis on metabolic rate, Reeds et al. (1980) correlated heat production to protein synthesis and demonstrated that approximately 21% of heat production could be attributed to protein synthesis in young pigs fed between maintenance and three times maintenance. Lobley et al. (1987) reported that for cattle fed between maintenance and 1.6 times maintenance, 19% of total heat production was due to protein synthesis. McBride and Kelly (1990) measured protein synthesis and estimated that it contributed 21 to 25% to total heat production of steers. Energy required for protein oxidation ranged from 20% to 6% (Lobley et al., 1987) of that required for synthesis for fasted steers and steers fed at 160% maintenance.

As stated above, the cost of protein synthesis and degradation may vary greatly with age and nutrient intake. Since this degradation may be viewed as an inefficiency, the increases in degradation at different ages and nutritional states could therefore contribute to the inefficiencies inherent in animals and therefore may potentially be an important contributor to differences in the efficiency of ME utilization.

1.2.2.2 Sodium-Potassium Transport. Transport of ions accounts for a significant portion of basal energy expenditure (Milligan and Summers, 1986), with the Na+, K+, transport system accounting for the majority of the cost of transport. The energy cost associated with Na+, K+ transport may be viewed as the cost of maintaining ionic homeostasis, membrane potentials, and the ionic gradient necessary to sustain nutrient uptake through this process (Summers et al., 1988). For example, co-

transport of an animo acid or sugar into a cell involves the movement of one Na+ down its transmembrane gradient (Alberts et al., 1989). The ion gradient is maintained by the action Na+, K+ - ATPase which simultaneously moves three Na+ out of the cell and brings two K+ in. The energy expenditure associated with this phenomena is 1 ATP (Milligan and Summers, 1986).

Since ion transport is involved in the transport of amino acids into the cell, it follows that energy transformations and ion transport in animals are intimately linked (Milligan and McBride, 1985), and therefore ion transport is likely a significant contributor to heat production of the animal. This speculation is supported by McBride and Kelly (1990) who commented that the energy cost of protein synthesis is proportional to the energy costs associated with Na+, K+-ATPase activity. Gill et al. (1989), with the use of a simulation model, concluded that Na+, K+ - transport accounts for 18-23% of the whole body ATP use in young sheep which is more conservative than earlier estimates which assigned values between 30 and 40% (Baldwin 1980) to this process.

In a review of a number of trials Milligan and McBride (1985) reported that Na+, K+-ATPase activity is responsive to the physiological status of the animal. For example, greater energy expenditures in support of Na+, K+ transport have been observed in lactating animals (Gregg and Milligan, 1982), in tissues from cold exposed animals (Guernsey and Stevens, 1977; Gregg and Milligan, 1982), humans in a diseased state (Butterfield et al., 1978) and when nutrient intake has been increased (Flier et al., 1981; McBride and Milligan, 1985). The effect of growth factors on Na+, K+ transport activity was investigated in an *in vitro*

trial (Rosengurt, 1981). In this experiment the exposure of cultured animal cells to mitogens caused a rapid increase in the rate of flow of Na+ into the cell. This resulted in an increase in Na+, K+ pumping, hence Summers et al. (1988) suggested that the greater energy expenditure of younger growing animal on Na+,K+ transport may be related to an elevated intracellular Na+. These speculations, however, have not been confirmed.

Unfortunately, estimations of the contribution of Na+, K+ - ATPase activity have been restricted to *in vitro* studies. Hence, caution must be used in interpretation of the data (MacRae and Lobley, 1986). They are, however, believed to be a significant contributor to the heat increment of feeding and therefore may have the ability to significantly influence whole-animal energy expenditure and hence the energetic efficiency of productive functions (McBride and Kelly, 1990).

1.2.2.3 Volatile Fatty Acid Production and NADPH Deficiency. A negative relationship has been shown between the proportion of acetic acid in the rumen fluid and the efficiency of ME utilization for fattening (Blaxter, 1962). Since more fibrous food will result in a greater acetate to propionate ratio within the rumen (Ørskov, 1975), it has been suggested that this may also partially account for the large differences in the efficiency with which ME is used between animals fed concentrates or forages. Much of this speculation has been derived from an experiment performed by Armstrong et al. (1958), in which mixtures either high or low in the proportion of acetic acid were infused into sheep. It was concluded that the utilization of volatile fatty acid (VFA) mixtures for fattening could be predicted on the basis of direct proportionality of

response to the individual acids. MacRae and Lobley (1986) commented that since there is an obligatory requirement for NADPH in the conversion of acetate to fat, adequate glycolytic precursors are required for its production through either the pentose phosphate pathway or from reactions associated with TCA-cycle intermediates. In the ruminant the primary precursors available for these pathways are propionate and glycogenic amino acids thus, when propionate is limiting, amino acids are required for acetate utilization (MacRae and Lobley, 1986), thereby changing the dynamics of metabolism in the animal and possibly affecting energy costs. Although this concept has been supported by the modelling results of Black et al. (1987) there have been conflicting reports on this hypothesis. Black et al. (1987) suggested that the effect of acetate on the efficiency of utilization of energy may be dependent on the diet, with acetate being more efficiently utilized with concentrate diets than with forage-based diets. Ørskov et al. (1979), however, found no significant differences in the HIF above maintenance in lambs sustained on infusions of nutrients containing VFA ratios of acetate: propionate: butyrate ranging from 75:15:10 to 45:45:10 and suggested that the results from Armstrong et al. (1958) may have been misleading as they were calculated from molar proportions rather than proportions of combustible energy supplied by the three VFA's. Recently, Ørskov et al. (1991) performed a similar experiment in steers and again found that the efficiency of ME utilization was not affected by different molar proportions of acetate and propionate.

In summary, the results of various workers (Armstrong et al., 1958; Blaxter, 1962; Black et al., 1987) support the concept that a shortage of glucogenic material may affect efficiency of ME utilization in ruminant

animals, however, Ørskov's experiment (1979) indicates that there is disagreement in the area and underlines the need for more comprehensive work.

1.2.2.4 Substrate Cycles. In situations where acetate cannot be completely utilized, substrate cycles may be stimulated to effect an energy loss with no obvious benefit to the animal (Lobley, 1986) thereby possibly affecting the efficiency of ME utilization. It has been suggested that these substrate cycles may, in part, be regulated by the availability of nutrients (MacRae and Lobley, 1986). These seemingly 'fultile' cycles and their subsequent energy expenditure are of interest to animal biochemists in assessing their contribution to maintenance requirements (Baldwin, 1980). Leng (1989) also suggests that an excess of acetogenic substrates could result in an increase in heat production, the implication being that this is achieved through substrate cycles. Substrate cycles in the glycolytic pathway have been the main focus of attention. In particular, cycling between fructose 6-phosphate and fructose 1,6-diphosphate (Summers and Milligan, 1988) may be important and has been shown to have the ability to increase 13 fold (Challis et al., 1984).

Although the energy expenditure of individual substrate cycles may be relatively small, it is possible that if several such substrate cycles were to respond at the same time, the overall effect of heat production may be significant (Challis et al., 1985). The potential importance of substrate cycles is demonstrated by Reeds et al. (from Milligan and Summers, 1986) who estimated that the combined contributions of substrate cycling from glycolysis, triglyceride turnover, and the Cori cycle was

approximately 7.5% of ATP turnover in the young pig.

1.3 Effects of Cold Stress

1.3.1 The Effect of Cold on Digestibility

In a number of trials over the last two decades, a decrease in the digestibility of forages in cold-stressed sheep (Kennedy et al., 1976, 1978, 1982) and cattle (Young and Christopherson, 1974; Christopherson, 1976) has been observed. In the study of Christopherson (1976) experiments were conducted involving calves and sheep held in ambient temperatures of -17 and -10 °C respectively in comparison with similar animals held at 16 - 20 °C indoors. The exposure to cold resulted in a decrease of .21 units in dry matter digestibility per degree celsius drop in environmental temperature for the calves and .31 units per degree celsius for the sheep. Ames and Brink (1977) estimated dry matter digestibility was lowered by .14 digestibility units per degree celsius fall in temperature in mature cattle however Christopherson (personal comm.) suggested more recent estimates of .10 units decrease per degree celsius degree in temperature for steers and mature cows. These data suggest that the effect of temperature on digestion may be following the general principle that animals of a larger body size are less likely to be affected by environmental changes than small animals (Kleiber, 1961). The rate of passage of digesta, or conversely, mean retention time, has attracted much attention since it is believed that the shorter retention time of particulate digesta in the rumino-reticulum is likely responsible for limiting the time available for fermentation of the more slowly degraded components of the diet (Kennedy et al., 1976; Kennedy et al.,

1986a). Kelly and Christopherson (1989) reported that animals exposed to cold temperatures (0 to 2 °C) exhibited declines in dry matter and organic matter digestibilities however there was no change in postruminal digestibility of dry matter or organic matter. This supports Kennedy et al. (1977), who reported cold exposure reduced total mean retention time primarily through reduction of the mean retention time in the rumen. This increase in the rate of passage occurs primarily in the rumen with no changes being observed in the hind gut.

The reduction in rumen turnover time during cold exposure, may be partly due to increased motor activity of the gastrointestinal tract (Kennedy et al., 1986a). Using five ruminally cannulated Holstein cows, Atteberry and Johnson (1969) found cows exposed to 2 and 18 °C had significantly greater amplitudes of rumen contractions than cows exposed to 38 °C. The frequency of contractions were also greater, however this effect was not significant. Lirette et al. (1988) found that contraction frequencies of the rumen and reticulum were increased by 49 and 55%, respectively, when steers were exposed to acute cold (-20 °C). This increased forestomach motility during cold exposure would be expected to enhance the rate of passage of small particles from the rumen (Christopherson and Kennedy, 1983). Okine and Mathison (1991), however, report that frequency of contractions may not be as closely related to passage rate as the amplitude and duration of the contractions, however the effect of temperature on amplitude and duration of contractions requires investigation.

The mechanisms which bring about the temperature induced changes in motility have as yet not been elucidated, however it has been suggested

that increased frequency of contraction of the ruminoreticulum during cold exposure involves increased neural activity from the gastric centre in the medulla oblongata (Leek and Harding, 1975). Kennedy et al. (1986a) also suggest that various endocrine changes may modify the sensitivity of the reflex neural pathways controlling motility. Thyroid hormone has been shown to increase rate of passage (Kennedy et al., 1977) while epinephrine will generally inhibit ruminoreticular motility. A host of other hormones have also been implicated as effectors of ruminoreticular function however these endocrinological as well as the neural mechanisms encompass an area which is beyond the scope of this review.

1.3.2 End Products of Digestion

In various experiments it has been noted that certain products of digestion are altered in cold stressed animals. Kelly and Christopherson (1989) found that cold induced an increase in total VFA production in the rumen. A depression in molar proportions of acetate to propionate have also been observe (Kelly and Christopherson, 1989; Kennedy and Milligan 1978). This depression, however, was not observed in an earlier study (Kennedy et al., 1976). An important implication of this is a potential increase in efficiency of utilization of ME for growth in the cold since propionate may be used more efficiently for growth than acetate (Van Soest, 1982).

Kennedy et al. (1982) reported reduced rates of rumen NH_3-N production from feed and endogenous protein sources in cold treated sheep given chopped brome-grass diets, however this trend was not observed in the lucerne or barley-canola seed meal diets. This reduction in rate of

rumen NH_3-N production in cold treated animals eating brome grass was also observed by Kennedy and Milligan (1978) and Kelly et al. (1989). Since the time available for fermentation is reduced in cold-exposed animals, decreased ruminal digestion of protein is expected to result in a lower rumen NH_3-N production (Ørskov, 1982). Thus far there have been no detectable changes in the quantity of microbial dry matter or N synthesized in animals exposed to different temperatures, however Kennedy (1976) did note a 12.5% increase in the efficiency of microbial synthesis (g microbial N/kg organic matter apparently digested in the stomach). This is in agreement with the suggestion of Lindberg (1983) that efficiency of microbial synthesis may be related to the dilution rate in the stomach. Similar responses were observed by various workers (Kennedy and Milligan, 1978; Kennedy et al., 1982, 1986) however this effect was not always significant (Kelly et al., 1989).

There have been reports of increases in amount of escaped dietary protein in animals exposed to cold (Kennedy and Milligan, 1976; Kelly et al., 1989a). Kennedy et al. (1986b) found that cold exposure tended to increased the amino acid content of non NH_3-N in the duodenum by 8 to 17% for sheep on chopped diets with valine, glycine, alanine and cystine being significantly greater. In a previous experiment, Kennedy et al. (1982) through the use a ^{35}S as a microbial marker demonstrated, that the increased flow of non NH_3-N in the cold was principally due to undegraded dietary protein not microbial N. Increases in amino acid flow to the intestine in cold acclimated sheep were observed by Kelly et al. (1989b), with valine, isoleucine and leucine delivery being significantly greater in sheep held in the cold environment as opposed to the warm. This

increased escape of amino acids, along with a potentially improved efficiency of microbial synthesis, would result in an increase of non NH_3-N entering the small intestine and consequently an increase in non NH_3-N absorption in the post-ruminal tract. This increase in non NH_3-N absorption would help to maintain the nitrogen economy of sheep exposed to a cold environment (Kelly and Chrisropherson, 1989).

In addition, an increase in the amount of dietary protein escaping degradation may increase the flow of essential amino acids to the small intestine, since microbial protein is considered to be deficient in several essential amino acids (Lobley, 1986).

1.4 Diet by Temperature Interaction

Egan (1977) found evidence that with low nitrogen, low digestibility diets, unfavourably low protein:energy ratios could be developed in sheep. It was proposed that where the protein to energy ratio is unfavourable, intake is limited by the protein insufficiencies. This protein:energy ratio may be a significant factor when dealing with animals in a temperate climate. A cold-stressed animal will oxidise acetogenic substrate for heat production and therefore the ratio of amino acids to energy in the balance of nutrients available for production will be higher than in an animal in its zone of thermoneutrality (Leng, 1989). In the absence of cold stress animals being fed a diet with an imbalance of protein to energy must utilize this excess substrate or reduce their feed intake (Leng, 1989). If possible, this "extra" energy could be utilized in the previously discussed futile cycles in increased ion transport, or some other mechanism, thereby decreasing the efficiency with which the ME is

utilized. Ames and Brink (1977) suggested that decreased rates of gain during thermal stress could by minimized by adjusting dietary protein for the thermal environment. Leng (1989) suggests that this imbalance in the ratio of protein to energy in animals in tropical climates is a major contributor to the decreased rates of gain observed in these countries. Acetate is used less efficiently than propionate by the animal (Baldwin, 1980) hence a decrease in the acetate:propionate ratio which is seen in the cold could increase the animals energetic efficiency. In addition, it has been suggested that a lack of glucogenic precursors, such as propionate, may affect the energetic cost of the animal (MacRae and Lobley, 1986). Finally, an increase in non NH_3-N in the cold may improve the efficiency of the animals.

In light of the above observations, it was hypothesized that; 1) protein supplementation would increase the efficiency of ME utilization, and 2) the response in energetic efficiency would be dependent upon environmental temperature. Hence the objectives of the present study were to; 1) determine the effect of RDP and UDP supplementation on the efficiency of ME utilization in lambs fed a low protein diet containing straw and barley and, 2) compare the effect of the above treatments in animals subjected to cold and warm ambient temperatures.

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II. THE EFFECT OF BYPASS PROTEIN SUPPLEMENTATION ON THE ENERGETIC EFFICIENCY OF LAMBS IN COLD AND WARM ENVIRONMENTS

2.1 Introduction

Supplementation of low quality forages with a rumen undegradable protein (UDP) supplement will often result in increased voluntary intake (Yilala and Bryant, 1985; Brand et al., 1991) live-weight gain (Yilala and Bryant, 1985; Hennessy and Williamson, 1990) and feed efficiency (Veira et al., 1985; Hennessy and Williamson, 1990; Petit et al., 1991) in ruminant animals fed such diets. There is great interest in this area since it implies the possibility of utilizing low-quality forages which otherwise have only been of limited use in production diets. The mechanisms which bring about the observed production responses are yet to be determined since the interpretation of many of the results are confounded by differences in voluntary intake and type and quantity of protein fed. It has, however, been suggested that supplementation with a bypass protein increases the efficiency of energy utilization (Yilala and Bryant, 1985; Gill et al., 1987). Unfortunately, although there is some research on the effect of dietary protein on the energetic efficiency of animals (Walker and Norton, 1971; Close et al., 1983), research with ruminant animals is limited (Walker and Norton, 1971; Blaxter and Boyne, 1978; Ortigues et al., 1990).

Over the years there have been inconsistencies in responses to bypass protein when trials are performed in different climates, with animals in tropical climates having seemingly greater and more consistent

responses to UDP supplementation than animals in more temperate climates (Leng, 1989). Leng (1989) suggests that this effect may in part be due to differences in the proportions of various nutrients available for production brought about by the differences in environmental temperatures. Since animals exposed to colder temperatures will use more energy for maintaining thermoneutrality, there will be less energy available for production, thereby changing the protein:energy ratio of nutrients available to the tissue. There have, however, been few comparative studies to explore this possible diet by temperature interaction (Ames and Brink, 1977). Since Canadian winters generally provide an environment of extreme cold stress which can adversely affect production levels of domestic animals, any interaction between dietary protein and environment merits much attention.

In light of the above observatons, the hypotheses of this study were; 1) protein supplementation would increase the efficiency of metabolizable energy (ME) utilization and 2) the response to bypass protein supplementation would be dependent upon environmental temperature. Thus the aims of this study were to; 1) determine the effect of rumen degradable protein (RDP) and rumen undegradable protein (UDP) supplementation on the efficiency of metabolizable energy (ME) utilization in growing lambs fed a low protein diet containing straw and barley grain and 2) compare the effect of the above treatments in animals subjected to cold and warm ambient temperatures.

2.2 Materials and Methods

2.2.1 Animals and Housing

Forty-eight Dorset crossbred lambs (mean weight 22.5 ± 2.6 kg) of equal numbers from both sexes with no antibodies to *Coxiella burnetti* infections were purchased for this experiment. Lambs were dewormed (Tramisol Sheep Wormer Oblets; Cyanamid, Canada Inc. Markham, ON.) and vaccinated with Covexin-8 (Coopers Agropharm Inc., Ajax, ON.) for prevention of clostridia infections (*Cl. chauvoei, Cl. septicum, Cl. haemolyticum, Cl. novyi, C. perfringens* type B, type C and type D; *Cl. tetani*) before being transported to the Laird McElroy Environmental and Metabolic Research Centre at the Edmonton Research Station.

On arrival animals were held in an outside, covered pen and fed chopped hay and whole barley for 7 days. The lambs were then shorn, weighed and blocked into three groups according to live weight and with equal numbers of males and females in each group. Two males and two females from each group (12 in total) were randomly selected to be slaughtered to establish initial body composition. These animals were held in an indoor stable (21 ± 1.8°C). The remaining 36 lambs were then split into 12 groups of three, with each group including one animal of the same sex from each live weight group. There were thus two groups of males and two groups of females for each of the three dietary treatments.

The lambs were placed in either a 6.1 x 7.3 m environmentally-controlled chamber or an indoor stable, both at room temperature. Animals were then fed a diet of chopped barley straw (*Hordeum vulgare*) and whole barley for another 7 days. At this point the temperature in the chamber

was reduced to 4.7 ± 1.7 °C, groups of lambs were assigned one of three diets (Table 2.1), and the 12 animals for initial body composition were slaughtered. Within each location, half of the animals were contained in metabolism crates and the other half were held in floor pens. While on the floor, the groups of three animals were held in a single pen. Animals in floor pens were moved to metabolism crates and animals in crates were placed in floor pens at approximately 10 day intervals. Shavings, used for bedding in the floor pens, were replaced approximately once weekly. Floor pens in the cold chamber (1.2 X 1.2 m) were slightly smaller than those in the stable area (1.8 X 1.8 m).

2.2.2 Feeding

Lambs were fed a basal diet of 50% chopped barley straw, 30% whole barley grain and 20% of a supplement containing rolled barley and either canola meal (*Brassica campestris*), Whitefish meal from British Columbia or no protein supplement (control diet) (Table 1.1). The canola meal and fishmeal diets were formulated to be isonitrogenous and isoenergetic while the control diet was of a lower nitrogen content. Animals held in the stable and cold chamber were offered diets at levels of 80 g dry matter/kg of $BW^{.75}$ and 90 g dry matter/kg $BW^{.75}$ daily, respectively. Straw, barley and supplement were weighed separately for each lamb, mixed and the total amount offered in two equal feedings at 8:00 and 16:00 h daily. Any orts were removed and the weight recorded. If lambs refused some of the ration the amount offered on the subsequent day was reduced so that orts did not exceed 10% of the amount offered. The amount offered was then gradually increased until lambs were eating at the same level as the rest of the

experimental animals. Lambs were weighed every 10 days and feed intake adjusted accordingly. Animals were fed individually in metabolism crates or through the use of headgates in the case of lambs in floor pens. Fresh water was provided daily and offered *ad libitum*.

2.2.3 Fecal and Urine Collections

Five-day metabolism trials were conducted on the lambs held in the metabolism crates at two different times during the study. The first period commenced after a 2 week adaptation period to the diets and temperatures. The balance trials were initially performed on only one-half of the animals in each temperature and dietary treatment. Once this was completed, animals were switched from floor pens to metabolism crates and five-day collection periods were performed for the second set of animals. A second balance trial was performed on all lambs approximately 20 days after the first one.

Representative samples of diets and any orts, taken and composited daily, were dried and ground through a 1 mm screen. Total feces and urine output were measured daily. Twenty-four hour feces output was collected and a 10% aliquot was taken and stored at -20 °C. After the 5-day collection period, aliquots were pooled, dried at 100 °C and ground through a 1 mm screen for analyses. Twenty-four urine output was collected over 10 ml 5N HCl, weighed and an aliquot was taken and stored at 5 °C. At the end of the collection period, subsamples were pooled and frozen at -20 °C for later analyses.

2.2.4 Indirect Calorimetry and Methane Measurements

For these measurements the three lambs from each treatment were placed in a 1.5 X 1.5 X 0.92 m chamber. The chamber was locally constructed with plywood on three sides with the fourth side and the top being covered with two layers of plastic which allowed light to enter the chamber. The chamber sides were placed on approximately 2.5 cm of soft foam to prevent escape of air. Chamber negative pressure was checked every 4-6 h. For the 24-hour measurement period, animals were placed in the chamber in the evening. The feed was placed in the chamber at the same time however lambs did not have access to it until 08:00 the next morning when the headgates were opened with a string pulled from the outside, allowing lambs access to the feed. The total daily amount was given in this feeding to avoid opening the chamber partway through the 24-hour measurement.

Two calorimetry measurements were taken during the 85 day trial, each in the week following the digestibility measurements. However for the females fed fishmeal and held in the stable area, the measurement which took place after the first balance trial was invalid due to problems with the equipment. The second measurement for the females fed the control diet in the cold chamber was also not used for similar reasons. As well, for the males held in the stable area and eating the control diet, one of the lambs was not eating at the time of the first calorimetry measurement hence this animal was not included in this measurement leaving only two animals for this particular observation.

Oxygen consumption was measured with a single-circuit Servomex paramagnetic oxygen analyzer (Servomex Instrument Company, model #540A,

Crowbridge, U.K.). Carbon dioxide production and methane production were measured with Beckman non-dispersion infrared analyzers (Beckman Instrument Company, Model #864, Fullerton, C.A., U.S.A.). Flow was measured with a Fischer and Porter variable area flow meter (Fischer and Porter Instrument Company, model 10A 3553A. Warminster, Penn., U.S.A.). This was done with an open-circuit calorimetry system (Young et al., 1975) attached to the animal chamber. Data from the three gas analyzers was taken with a Datalogger (Data Electronics Corp., Melbourne Australia, model DT100) every 10 s and averaged over a 15 min period. A locally produced piece of software was used to capture the data on a personal computer. Room air measurements, temperature and barometric and manometric pressure were also taken every 4-6 h and lambs were observed for signs of stress (eg. panting, restlessness) every 4-6 h.

Concentrations of the gases in the standard were .995% CO_2, .09% CH_4 and 19.94% O_2. Outside air was also used as a standard (20.92% O_2, .03% CO_2, 0% CH_4). Readings of standards were recorded at the beginning and end of every 24 h measurement. Calorimetry equipment was calibrated with the iron-burn method (Young et al., 1984) approximately once every week.

Total heat production (kcal/day) was calculated as 3.866 x O_2 (l/d) + 1.200 x CO_2 (l/d) - 0.518 x CH_4 (l/d) + 1.431 x urine-N (g/d) (Brouwer, 1965). The ME content of the diet was estimated by subtracting the energy lost in feces, urine and methane from the gross energy intake. Heat production was then subtracted from the ME intake to give the energy retained by the lambs. Nitrogen balance was calculated from the digestibility balance trial and converted to energy retained as protein using an energy equivalence value of 5.59 kcal per gram protein from

Rattray et al. (1973). Fat retained as energy was then calculated using the relationship Retained Energy = Energy retained as protein + Energy retained as fat.

2.2.5 Blood and Rumen Samples

Ten ml blood samples were obtained via jugular puncture and collected in heparinized vacutainer tubes approximately 3 hours after the morning feeding on days 49 and 80 of the trial. Blood samples were centrifuged immediately at -4 °C and 3000 x g for 15 min. Plasma was then placed in scintillation vials and frozen at -20 °C. Rumen samples were collected at the same time as blood samples with an endotracheal tube. Rumen fluid was filtered through three layers of cheesecloth, placed in scintillation vials and stored at -20 °C.

2.2.6 Whole Animal Composition

At the onset of the trial the 12 initial slaughter lambs were weighed, euthanized with T61 euthanasia solution (Hoechst Canada Inc., Regina SA.), and the contents of the reticulo-rumen removed. Whole sheep were weighed and stored at -20 °C. Frozen lambs were moved to the Meat Research lab at the Edmonton Research station and cut into 15 x 10 cm pieces with a band saw. Cut pieces were ground through a 6 mm screen with a whole body grinder (Autio Manufacturing Oregon, U.S.A., model 801). Due to the impracticality of cleaning the grinding machine after each animal, approximately 300 g of a lower hind leg were put through the grinder last to ensure that if any contamination occurred, it would be uniform from animal to animal. The ground mixture was mixed thoroughly by hand and

then duplicate representative samples were taken from approximately 15 different areas of the ground carcass. These samples were weighed, double bagged and stored at -20 °C. Samples were then freeze dried, reweighed and processed further in a Waring blender to obtain a more homogenous mixture for determination of composition.

On day 85 of the trial, the remaining 35 animals were euthanized, their reticulorumen contents removed and the empty bodies were frozen at -20 °C. It was necessary to shear the frozen carcasses before cutting to prevent the wool from plugging the saw. The wool was then mixed with the frozen pieces of carcass as they were put through the grinder. Other than this, carcasses were processed in the same manner as described previously.

The concentration of energy, protein and fat of the initial slaughter lambs were related to body weight by regression analysis. Equations for fat, protein and energy content were then used to estimate the starting composition of each of the remaining experimental animals at the start of the experiment. Retained energy, fat and protein were then calculated as the difference between the calculated initial and measured final values. Energy retained as protein was calculated using a value of 5.59 kcal/g (Rattray et al., 1973). The remainder of the retained energy was assumed to be fat (9.31 kcal/g; Rattray et al., 1973).

2.2.7 In Situ Degradability

The degradability of the dietary components was determined with the nylon bag technique (von Keyserlingk and Mathison, 1989). One rumen-fistulated steer was adapted to a basal diet of 50% barley straw and 50% barley grain 2 weeks prior to trial. Feed was offered twice daily.

Bags were made from 7.0 x 5.5 cm pieces of nylon (Phentex, PE300 pore size 48 um B and SH Thompson and Co. Ltd., Toronto, Ont., Canada) which were folded in half and heat sealed (Audion Impulse Sealer, Audion Elektro, Packaging Aids Company, San Francisco) on two sides. One gram of ground (1mm screen), dried sample was placed in each bag and the last side was then heat sealed. A total of 14 bags (two bags per time of incubation) each of barley grain, canola meal supplement and fishmeal supplement were prepared. Twelve samples of each concentrate were suspended in the rumen in a polyester mesh bag and incubated for 2, 4, 8, 12, 16 or 24 h; the remaining two were 0 h samples. Eighteen bags of barley straw were prepared and 16 of these suspended and incubated in the rumen for 4, 8, 12, 16, 36, 48, 72 or 120 h; the remaining two were 0 h samples. Nylon bags were introduced into the rumen in reverse order (i.e. h-120 was introduced first) so that the bags were all removed and washed at the same time. The zero time samples were not introduced into the rumen, however they were washed with the rest of the nylon bags. All bags were washed simultaneously in the mechanical bag washer described by De Boer et al. (1987) and dried to a constant weight at 100 °C for dry matter (DM) determination.

2.2.8 Chemical Analyses

Dry matter determination of diets, orts, and feces was determined by drying at 100 °C to a constant weight. Meat samples were freeze dried (Vitris Company, Gardiner, N.Y. 12525) to a constant weight (approximately 3 d) and reweighed and then the calculated %DM was used to correct laboratory analyses to a fresh lamb weight basis. Nitrogen concentration

was determined for diet, orts, meat, feces and frozen urine samples with the macro-Kjeldahl procedure (AOAC 1984, Procedure #2.057). Nitrogen was determined on *in situ* samples while they were still in the bag; empty nylon bags were used to correct for the nitrogen content of the Phentex bag material. The same technique was used for nitrogen determination of frozen urine samples which were contained in 5 x 5 cm plastic bags. Energy content of all samples was determined in an automatically controlled adiabatic bomb calorimeter (Parr Instrument Company, Inc. Moline, Illinois, U.S.A.). Three 5 ml samples of urine were placed in 5 x 10 cm plastic bags and freeze dried before determinations of energy content. Bags were included in the measurement. Ten empty plastic bags were then used to determine the energy content of the bags alone. Acid detergent fibre (ADF) and neutral detergent fibre (NDF) were determined for all diet, ort and fecal samples by the method outlined by Goering and Van Soest (1970). The Goldfinch (AOAC, 1984. Procedure #24.005) method using petroleum ether was used to estimate of lipid content of the meat samples. Ash content of all samples was determined by placing 2 g samples in an ashing oven (Heavy duty Heating equipment Company, Wisconsin, U.S.A.) at 500°C overnight (AOAC 1984, procedure #7.009). Ammonia nitrogen concentration was measured in rumen samples (Fawcett and Scott 1960) and urea-N was determined in plasma samples using a colorimetric procedure based on the diacetyl monoxime method (Sigma Co., St. Louis, MO. procedure #535).

2.2.9 Statistical Analyses

The experimental design for this procedure was a 2 x 3 x 2 factorial

design which was analysed using the GLM procedure of SAS (1985). Main effects for the comparative slaughter trial were diet (*n=3*), temperature (*n=2*) and sex (*n=2*). For digestibility measurements, period effects (*n=2*) were also taken into account. Dry matter intake was used as a covariate, however it was removed from the model if insignificant (P>.10). There were three animals per replication with the exception that one animal died prior to the sampling period. Because of this mortality, the use of least square means was employed. For analyses of heat production, methane production, and retained energy from the indirect calorimetry-balance trial, all three animals per treatment were treated as one observation since all the animals in a treatment were measured together. Hence, in the 2 x 3 x 2 factorial experiment there were only two replicates per treatment for the indirect calorimetry measurements; one for each period.

All interactions were tested and, except for the temperature by diet interaction, were removed from the model if insignificant (P>.10). A multiple range test using Student Neuman Keul's procedure was performed to distinguish between mean values among dietary treatments.

The *in situ* disappearance of crude protein at each incubation time was calculated from the crude protein remaining in the bag after rumen incubation. The disappearance rate (p) was fitted to the equation derived by Ørskov and MacDonald (1979) where t represents the incubation time.

$$p = a + b(1 - e^{-ct})$$

The soluble (a) and slowly degradable (b) portions of the feed as well as the rate constant of degradation (c) were estimated by an iterative least

squares procedure on SAS (1985), and best fit values were chosen using the smallest sum of squares after convergance (Khorasani et al., 1989).

Estimated degradability of the crude protein (EDCP) was calculated using the following equation (Ørskov and MacDonald 1979):

$$EDCP = a + bc/(c + k)$$

The frational outflow rate (k) used to calculate the estimated degradability of crude protein was 5%/h.

2.3 Results

Approximately 2 weeks after the start of the experiment, one lamb died of causes unrelated to the trial. Thus there were only two animals in the male lamb group fed the canola-supplemented diet in the cold.

Although the animals within each temperature treatment were offered a set level of feed daily, some animals did not eat all that was set before them. When this occurred, the amount of feed offered daily was reduced to a level such that all feed was eaten. The feed offered was then gradually increased until the lambs were eating at the same level as their counterparts. The result of this was that not all lambs, within their environment, ingested the same amount of feed per kg metabolic body weight.

2.3.1 Feed Composition and Intake

The ingredients and chemical composition of the diets are presented in Table 2.1. The canola and fishmeal diets were isonitrogenous and isoenergetic ($P>.10$). These diets contained 55 to 62% more ($P<.01$) protein than the control diet.

The estimated fractions of the rapidly (fraction A) and slowly (fraction B) degradable crude protein of the dietary ingredients and the rate of degradation of fraction B are presented in Table 2.2. The rumen degradation characteristics of canola meal and fishmeal were not individually determined since the complete concentrate was of primary concern. From these values, and assuming a fractional outflow rate from the rumen of 5%/h, total UDP content of the control, canola and fishmeal

diets was calculated as 1.6, 2.7 and 4.1%, respectively. The corresponding RDP contents of the diets were 5.8, 8.8 and 7.9%.

As planned in the experimental design, the daily intakes, of dry matter, gross energy (GE), organic matter (OM), N, ADF and NDF were greater for the animals in the cold environment ($P<.01$) than the ones in the warm environment (Table 2.3). Intakes remained the same for both sexes ($P>.10$). Lambs receiving the canola and fishmeal diets had a 57 and 60% greater intake of nitrogen (N) than the lambs fed the control diet, respectively (Table 2.3). Animals eating the fishmeal supplement ingested less ($P<.05$) ADF and NDF than lambs in the other two groups.

2.3.2 Apparent Digestibilities

The digestibilities (Table 2.4) of DM, GE and OM were lower in the cold, although digestibility of N, ADF and NDF were not influenced by environment. Protein supplementation improved the digestibility of N ($P<.01$), and in the case of canola meal, increased energy, dry matter digestibility and neutral detergent fibre digestibility. Fishmeal supplementation decreased ADF and NDF digestion ($P<.05$). Organic matter digestibility was not affected by diet. Although the digestibility of the fishmeal and control diets increased in the warm environment, the digestibility of DM, GE, N and NDF of the canola-supplemented diets remained the same or decreased in the warm when compared to the cold temperature, hence there was a trend ($P<.10$) towards a diet by temperature interaction. Females tended ($P<.10$) to have a greater digestibility of DM, OM and fibre than males.

2.3.3 Animal Performance

There were no differences in initial weights between lambs placed in the cold and warm environment (Table 2.5). Animals held in the warm environment, however, were 10% heavier (P=.01) at the end of the trial than those exposed to the cold environment. This was also reflected in a tendency for a reduced (P<.10) daily gain in the cold. The gain to dry matter intake ratio tended (P=.06) to be improved by 18% at the higher ambient temperature.

There were no differences in initial weights among the lambs on the different dietary treatments, however lambs fed the control diet had a lower (P=.04) final weight than those fed the fishmeal diet. Daily gains tended to increase with canola and fishmeal supplementation. Protein supplementation did not influence gain to dry matter intake ratio (P=.22).

Males weighed more than females at the beginning (P=.03) and at the end (P<.01) of the trial, but no differences in daily gains or feed efficiency between the two sexes were observed.

2.3.4 Nitrogen Partitioning

Intake of N was higher (P<.01) in the cold as was urinary nitrogen excretion (P=.05) (Table 2.6). Retention of N was 30% lower (P=.04) in the cold than in the warm. The control diet also resulted in less (P<.05) N being excreted in the urine and feces and less (P<.01) retained N than when the two high protein diets were fed. Plasma urea nitrogen and rumen NH_3-N concentrations were unaffected (P>.10) by temperature, however they were influenced by diet (P<.01). Rumen NH_3-N concentrations were greatest (P<.01) for the canola diet and lowest for the control diet with fishmeal-

supplemented animals having intermediate concentrations. Plasma urea-N was increased ($P<.01$) approximately 94 and 115% by canola- and fishmeal-supplementation, respectively, however, there was no difference between the canola meal and fishmeal supplemented animals. No differences in plasma urea-N and rumen NH_3-N were detected between males and females.

2.3.5 Methane and Urinary Losses

Methane production was not ($P>.10$) influenced by environmental temperature, although methane production as a percentage of DE tended to increase ($P=.06$) in the cold (Table 2.7). Neither diet nor sex influenced methane losses.

Urinary energy losses were increased with the lower temperature and higher on the two high protein diets, however, energy losses in the urine were not affected by sex.

2.3.6 Energy Partitioning

The ME intakes for the comparative slaughter technique were calculated from the average daily feed intake throughout the feeding trial, whereas for the calorimetry trial the actual intakes on the day of the measurement were used. For this reason the two intakes are not the same in Table 2.8. Intakes of ME were 7 and 10% higher for lambs eating the canola diet than the control diet in the comparative slaughter and calorimetry measurements, respectively. For the calorimetry measurements, the females had a greater ($P=.02$) ME intake than the males did.

Heat production was 7% lower ($P=.02$) for lambs in the cold than for lambs in the warm (Table 2.8) and 8% greater ($P=.04$) for lambs eating the

canola than the control diet in the comparative slaughter measurements. No differences in heat production were detected with calorimetry measurements.

On the basis of the comparative slaughter measurements energy, fat and protein retentions were lower ($P<.05$) for the cold-treated animals than for the warm- treated animals (Table 2.8). Similar differences were noted for total energy retention and energy retained as fat with the calorimetry technique, however, these differences were insignificant. Energy retained as protein tended to be increased by 30% ($P=.06$) with fishmeal-supplementation according to comparative slaughter and by 228% according to calorimetry procedures. Energy and fat retention were not affected by diet. On the basis of comparative slaughter, sex had no effect on energy retention or partitioning, however, the calorimetry measurements demonstrated a trend for greater fat ($P=.09$) retention in females than males.

2.4 Discussion

2.4.1 Intakes

It is recognized that the maintenance requirements of animals in colder ambient temperatures are greater than for those held in thermoneutral environments (Young et al., 1989), hence animals in the cold environment were offered slightly more feed than in the warm. The lambs in the cold were offered 11% more DM, however, actual intakes were only 6% greater (Table 2.8). The lower final weights demonstrated by animals in the cold (Table 2.5) suggest that this was inadequate to compensate for the effects of cold on these animals.

2.4.2 Rumen Degradability

There is large variability in the estimates of the A and B fractions of the straw as well as the degradation rate, however, this large error with straw has been observed by other workers (von Keyserlingk and Mathison, 1989). The estimated degradability of the crude protein in barley, derived from information on the barley concentrate at a fractional outflow rate of 5%/h, was 93%, which is in agreement with values presented by De Boer et al. (1987). Since the degradability of the crude protein of barley was estimated, calculations can be made to determine the approximate degradability of the actual protein supplements used. Such calculations suggest that the degradability of the CP of the canola meal was approximately 72%. This is in agreement with values presented by both De Boer et al. (1987) and Khorasani et al. (1989). The calculated degradability of the crude protein of fishmeal, estimated at 2%, is

relatively low compared to the value of 20% suggested by NRC (1985), although the degradability of fishmeal is highly variable (Hussein and Jordan, 1991b). However, due to the high percentage (70%) of barley in the fishmeal supplement, it is expected that the A and B fractions, as well as the rate of degradation of the B fraction, would closely follow the degradability characteristics of the barley. Thus estimations of the degradability of fishmeal will be of limited accuracy when calculated in this manner.

Rumen NH_3-N levels can be directly related to the degradation rates of the crude protein (Hussein and Jordan, 1991a). Hence, the greater NH_3-N concentrations of the fishmeal- compared to the control-supplemented lambs confirms a greater amount of RDP in the fishmeal diet. Further, relatively high concentrations of plasma urea-N and rates of nitrogen retention (Table 2.6) imply that, although the fishmeal may have been relatively undegradable in the rumen, it must have been available for absorption in the small intestine. Similarly, the greater rumen NH_3-N concentrations in the canola-supplemented lambs confirms that there was more RDP with this diet than in either the control or fishmeal diets.

A number of workers have observed a decrease in the efficiency of microbial protein synthesis when fishmeal was added to the basal diet in sheep (Mercer et al., 1980; Hussein et al., 1991) and cattle (Cecava et al., 1991) which could be due to the lower rumen NH_3-N concentrations when fishmeal is fed (Cecava et al., 1991). This should not have been a problem with either the fishmeal and canola diets since rumen NH_3-N were greater than 5 mg/dl, which Satter and Slyter (1974) indicated was sufficient to support maximum growth rates of rumen bacteria. The

concentrations of the rumen NH_3-N of the lambs on the control diet may however, have been insufficient for maximal fermentation on this basis. The recommendation of Satter and Slyter (1974) was, however, obtained from the results of *in vitro* studies and is far below the value of 23.5 mg/dl recommended by Mehrez et al. (1977) for maximal fermentation. The rumen NH_3-N concentrations of the fishmeal diet were less than 50% of the concentrations needed to achieve maximal fermentation, as proposed by Mehrez et al. (1977), hence it is possible that all three diets resulted in a less than optimal rumen NH_3-N concentrations for fermentation and microbial growth.

The control, canola and fishmeal diets provided 1.6 2.7 and 4.1% UDP, respectively. Male lambs gaining 80 g daily require 40 g UDP and 59 g RDP in the ration (NRC, 1985). Corresponding values for the female lambs are 35 g UDP and 59 g RDP, respectively. The control diet provided approximately 14 g UDP and 51 g RDP daily. The canola meal diet provided lambs with approximately 26 and 83 g UDP and RDP daily, respectively, whereas those fed the fishmeal diet received 39 g UDP and 75 g RDP. According to these estimates the diet of the control lambs only provided 40 and 86% UDP and RDP, respectively of the estimated requirements for this rate of gain and hence the lambs should have been deficient in both UDP and RDP. Matras et al. (1990), using regression analysis, estimated that the optimal proportion of UDP in growing lamb diets, containing 10.5% protein, was 50%. This recommendation was derived from the nitrogen utilization of growing lambs receiving a diet containing 35% cottonseed hulls and 65% cracked corn at three different levels of intake. The intermediate level of intake was similar to the intake level of this trial

(between 880 and 950 g/d). In light of the above observations, the proportion of UDP supplied by even the fishmeal diet may not have been adequate for maximum growth since only 34% of the total CP content of the diet was UDP.

2.4.3 Digestibility

Digestibilities of DM, OM and GE were reduced in the cold by .20, .21 and .11%, respectively, per drop in °C. Westra and Christopherson (1976) found a similar decrease in DM digestibility of .19 digestibility units per drop in °C. The effect of cold on OM digestibility was, however, lower than the reductions of .26 observed by Kelly et al. (1989), and .23 (Kennedy et al., 1982), both in sheep fed a basal diet of brome grass hay. Kennedy et al. (1982), however, found that the OM digestibility was not affected by temperature when sheep received a basal diet of alfalfa or concentrate implying that there was a diet by temperature interaction. The digestibility of ADF was not affected in this trial by environmental temperature which differs with results from other workers (Westra and Christopherson, 1976; Kelly and Christopherson, 1989). There was no decrease in N digestibility with cold-exposure; cold appears to have a variable effect on N digestibility (Westra and Christopherson, 1976; Kennedy et al., 1982). During cold exposure there is a reduced retention time of particulate and fluid digesta in the ruminoreticulum (Christopherson and Kennedy, 1983). This increased rate of passage, or conversely, reduced mean retention time, is responsible for limiting the time available for fermentation of the more slowly degraded components of the diet (Kennedy et al., 1986), hence the reduction in digestibility with

cold. Results from Kennedy et al. (1977) and Kelly and Christopherson (1989) indicate that the reduced total mean retention time is primarily a result of a reduction of mean retention time in the rumen, as opposed to changes in post-ruminal retention time.

The canola diet generally had the highest digestibility. Mehrez et al. (1977) proposed that lower ruminal NH_3-N concentrations could result in lowered digestibility brought about by decreased fermentation in the rumen, hence the lower ruminal NH_3-N concentrations in the control and fishmeal diets, as discussed previously, may have resulted in the reduced digestibilities observed with these two diets. However, the reduction in the digestibilities of ADF and NDF in the fishmeal diet was unexpected since previous workers have observed either an improvement in fibre digestibility (Hussein et al., 1991b) or no response (Petit et al., 1992b) with the addition of fishmeal to basal diets. Microbial growth, however, may still be limited with adequate concentrations of NH_3-N if concentrations of other nutrients are insufficient to maximize growth (Cecava et al., 1991). Cellulolytic bacteria require branched chain fatty acids for growth. These fatty acids are produced by non-cellulolytic bacteria from the branched chain amino acids (Yokoyama and Johnson, 1988) hence the decreased fibre digestibility in the fishmeal-supplemented lambs may have been a consequence of insufficient branched chain amino acids available to the rumen bacteria due to the large proportion of the dietary protein which escaped from the rumen.

Although the digestibilities of the control and fishmeal diets decreased with cold exposure, this decrease with the cold temperature was not observed in the canola diet. Thus there was a trend towards a diet

by temperature interaction in the digestibilities of DM, GE, N and ADF. Christopherson and Kennedy (1983) observed that the digestibility of forage diets, which tend to be fermented slowly, appear to be more susceptible to changes in rate of passage brought about by exposure to different temperature than concentrate diets. Although there were no differences in the roughage content of the diets, the above observation does suggest that all diets are not influenced to the same extent.

The reason for the trend for the greater digestibilities of DM, OM, ADF and NDF in the females than in the males remains unclear.

2.4.4 Productivity

Despite the lower digestibilities of DM and fibre in the fishmeal than in the canola meal diets, there was a tendency for the fishmeal-supplemented lambs to exhibit higher final weights and average daily gains than control lambs. Although increases in live weight gains with fishmeal supplementation have been observed by a number of workers (Klopfenstein et al., 1982; Gill et al., 1987; Petit et al., 1992a), in some cases (Gill et al., 1987; Ortigues et al., 1989) differences were detected only between UDP supplemented diets and a lower nitrogen control diet since no diets containing a more degradable source of protein were fed. Results from such trials suggest that the growth of animals was limited by a protein deficiency, but give no indication if UDP was essential. Further, in a number of trials (Gill et al., 1987; Veira et al., 1985, 1990) intake was not controlled, making it difficult to separate the effect of UDP supplementation on growth rate and efficiency from effects of nitrogen intake, per se, on performance.

Oldham and Smith (1981) did observe that protein supplements that largely escaped rumen degradation consistently supported higher weight gains than other, more degradable supplements. However, in the present trial, no differences in animal responses were detected between the UDP- and RDP-supplemented diets. These results are similar to those of Yilala and Bryant (1985) and Steen (1989) who also detected no response when bypass protein replaced rapidly degraded protein in the diet. In variance with Hennessy and Williamson (1990) and Petit et al. (1991), no significant differences in feed efficiency were observed with bypass protein supplementation.

Although the mechanisms responsible for improvements in animal production in response to bypass protein have not yet been elucidated, it is postulated that escape protein supplementation may result in an improved protein to energy ratio in the end products of digestion (Veira et al., 1988). A decrease in microbial N flow with escape protein supplementation has been observed in some circumstances (Hussein et al., 1991), however with this decrease total nitrogen flow to the duodenum has either remained the same (Lindberg, 1983; McCarthy et al., 1989) or increased (Titgemeyer et al., 1989; Cecava et al., 1991) with UDP supplementation. For example, Cecava et al. (1991) reported a 14% increase in total flow when a mixture of corn gluten meal and blood meal replaced soybean meal. Thus, the greater proportion of UDP supplied by the fishmeal diet may have resulted in an improved nutrient supply to the small intestine, thereby improving production.

A decrease in the acetate to propionate ratio from 2.12 to 1.74 was observed by McCarthy et al. (1989) when fishmeal replaced soybean meal in

barley-based diets in lactating cows although this effect was not observed by Cecava et al. (1991). A negative relationship has been shown between the efficiency of ME utilization for fattening and the proportion of acetic acid in the rumen fluid (Blaxter, 1962; Black et al., 1987). Ørskov et al. (1979, 1991), however, found no differences in the energetic efficiency of lambs sustained by infusions of mixtures of volatile fatty acids containing various proportions of acetic acid. Unfortunately, the concentrations of the VFA's in the rumen fluid were not measured in this experiment so it cannot be determined if differences in rumen VFA concentrations were related to the tendency for fishmeal-fed lambs to have a higher growth rate.

The adequacy of live weight gains as a measure of animal response is questionable. Although empty body gains may give us more accurate estimates of energy retention than live weight gains due to the removal of gut fill as a possible source of error (Thomas et al., 1988), neither measurement gives us an indication of the relative proportions of energy retained as fat or protein. This is demonstrated by results from Waldo and Tyrell (1980) in which the total energy retained in animals fed two different diets was the same, however, the body composition of the animals on the two diets differed. Steers receiving untreated silage supplemented with casein deposited 37% of their retained energy as protein and 63% as fat, whereas steers receiving the formaldehyde-treated silage supplemented with casein deposited 50% of energy as protein and 50% as fat. Although total energy retained was the same for all three diets in the present trial, the proportion of energy retained as protein was 29 and 25% greater for the animals eating the canola and fishmeal diets, respectively, than

for those eating the control diet. Other workers (Walker and Norton, 1971; Close et al., 1983; Gill et al., 1987) have also found that with increasing protein content of the diet, a greater proportion of total energy retained is retained as protein than as fat.

Leng (1989) suggested that the discrepancies in the results of experiments performed in tropical versus temperate climates may be a function of the effect of temperature on the protein:energy ratio of the end products of digestion. A cold-stressed animal will oxidise acetogenic substrates for heat production and therefore the ratio of amino acids to energy in the balance of nutrients available for production will be higher than in an animal in its zone of thermoneutrality (Leng, 1989). Leng (1989) also implies that the use of bypass protein may further improve this protein:energy ratio in the end products of digestion. On the basis of the above observations, it was hypothesized that the response to bypass protein supplementation would be greater in the warm than in the cold due to a more appropriate protein:energy ratio in the small intestine for absorption. In this experiment, however, no temperature by diet interactions on rate or efficiency of gain were observed. It is possible, however, that a response might have been observed if the animals in the warm treatment had been subjected to a higher temperature.

2.4.5 Methane and Urinary Losses

In the present trial, total methane production was not influenced by the cold environment. In addition, when expressed as a percentage of DE, energy lost as methane increased 17% ($P<.10$) with cold-exposure, which is in sharp contrast to observations from other workers (Graham et al.,

1959; Kennedy and Milligan, 1978) who noticed 20 to 25% decreases in total methane production in the cold. Although Blaxter and Wainman (1961) did find a decrease in methane loss with cold treatment with one steer, there was no response in the second steer. The effects of temperature on methane production were variable between 20 and 40°C (Rogerson, 1960). For example, at high intake levels, an increased environmental temperature reduced methane production, whereas at submaintenance intake levels no effect was noticeable.

Our results are also in variance with expectations of Christopherson (personal comm.) who observed that decreased digestibility of diets in the cold would also result in less substrate being available for methane production by microorganisms. Moreover, Okine et al. (1989) reported a negative correlation between passage rates and methane production, hence, since there are faster passage rates in cold-exposed sheep (Christopherson, 1989), a decrease in methane production with decreasing temperature might be expected in cold-treated animals (Christopherson, personal comm.). Further, an increase in the propionate to acetate ratio has been observed with cold-treated animals (Kennedy and Milligan, 1978) which may indicate a partial shift from a methanogenic to a propionic fermentation in the rumen (Fahey and Berger, 1988) in animals in cold environments.

The literature available on the effects of temperature on methane losses is limited. Of four research reports found in the literature in the area, in three of these only two animals were used (Graham et al., 1959; Rogerson, 1960; Blaxter and Wainman, 1961). In spite of this problem, some insight into the effect of temperature on methane losses

might be gained by looking at the DM intake in these trials. Results from Graham et al. (1959) indicate that temperature may not affect methane production in adult sheep at lower levels of intake (600 g/d), whereas methane production of sheep may decrease in the cold at intakes of 1200 and 1800 g/d. Rogerson (1960) and Blaxter and Wainman (1961) also found no response in methane production to temperature in two year old steers fed at submaintenance levels of intake. In the fourth trial, intakes of sheep, weighing between 59 and 69 kg were intermediate at 1400 g/d (Kennedy and Milligan, 1978) and methane production was decreased in the cold. The lambs in the present trial were eating between 880 and 950 g/d which can, for the size of the sheep, be considered an intermediate level of intake. This alone may not have been the cause of the lack of response, however, an additional consideration is that the sheep used in the trials of Graham et al. (1961) and Kennedy and Milligan (1978) were shorn every 7 and 18 days, respectively, whereas in the present trial lambs were shorn only once at the beginning of the trial. The effects of thermal insulation and behaviour will be discussed later, however, it is possible that the lambs in this trial may not have been truly cold-stressed. Thus the combination of an intermediate feed intake and an inadequate cold temperature may have affected the respone. On the basis of this we can conclude that: 1) cold environments do not always cause a decrease in methane production even though feed digestibility may be decreased and 2) the interaction between feeding level and temperature on methane production needs to be examined further.

Rogerson (1960) also observed that substitution of protein and carbohydrate supplements for one-third of the basal ration had no effect

on methane production. Diets also had no effect on methane production in the present trial.

Losses in urinary energy increased when environmental temperature was decreased. This agrees with results reported for sheep by other workers (Graham et al., 1959; Blaxter et al., 1959).

Diet also affected energy lost in the urine, with the losses in lambs receiving the lower protein diet being smaller than those receiving the higher protein diets. Again this has been observed by other workers (Matras et al., 1990; Ortigues et al., 1990).

2.4.6 Energetic Efficiency

In the present trial heat production decreased with cold-exposure. This decrease was unexpected since heat production in sheep has been observed to increase with exposure to cold temperatures (Graham and Christopherson, 1981). Although dry matter intakes were higher in the cold, ME intakes were lower, hence the reduction in heat production of the animals in the cold can be attributed to their lower ME intake since heat production is dependent on ME intake (Close et al., 1983). Heat production appeared to become independent of food intake only below 0°C in the trials of Graham et al. (1959) and Blaxter and Wainman (1961). This suggests that animals must be truly cold-stressed before heat production will increase independent of intake.

The behaviour of the lambs may also have had an effect on their heat production in the periods when they were in floor pens. At the beginning of the trial, when the lambs had been recently shorn, lambs in floor pens in the cold chamber were frequently observed huddled together. Such

activity would reduce the surface area for heat loss and aid in the conservation of body heat (Young, 1985). Since heat production by calorimetry was measured with three animals in a group in floor pens, this behavioural response could have greatly affected the heat production measurements from the calorimetry procedure. It could also have affected the longer term heat production measurements from the comparative slaughter technique since lambs were held in floor pens for half of the 85 day trial. The huddling behaviour was not observed later in the trial, however, when the fleece of the sheep had grown. At the end of the trial, wool growth was approximately 3.5 cm. The thermal insulation of the hair coat is of major importance in combatting cold stress (Young, 1981), hence the increase in insulation at the end of the trial, as well as the behavioural responses of the sheep may have decreased the animals lower critical temperature, thereby reducing the effect of the temperature treatment.

Protein supplementation did not affect the efficiency of ME utilization in this experiment (Table 2.8). These results are in agreement with Barry (1981) in young lambs and Close et al. (1983) in pigs. Results, however, have been inconsistent with other groups finding both increases (Blaxter and Boyne, 1978; MacRae et al., 1985), and decreases (Walker and Norton, 1971) in efficiency with increasing protein intake. Walker and Norton (1971) observed that the efficiency of ME use for growth decreased by 9 and 7%, respectively with medium and high protein diets in young lambs, however corresponding efficiencies of ME use for maintenance were 38 and 39% greater with the higher protein diets. In addition, Walker and Norton (1971) observed that the ME requirement for

maintenance was lower for the lambs on the medium-protein diet. Moreover, their high protein diet provided 55% more protein than that of ewe's milk, hence an imbalance in the protein to energy ratio could result in a further inefficiency. If there is an excess of protein in the ration, the animal may use the protein as an energy source. This would result in an increased loss of amino groups as urea and hence energetic efficiency may decrease (Walker and Norton, 1971).

Blaxter and Boyne (1978), in direct contrast to Walker and Norton (1971), found a trend for increasing efficiency of ME utilization for growth with increasing dietary protein concentration; efficiencies increased approximately 10% for every increment of 5% in protein ranging from 5 to 20%. The opposite trend was evident for maintenance, however these decrements were between 1 and 2% depending on the metabolizability of the diet. These workers, however, did find that energetic efficiency for growth was more related to the metabolizability of the diet than it was to protein content.

MacRae et al. (1985) reported a 26% increase in the efficiency of ME utilization for growth when casein was infused into the abomasum of mature wethers. MacRae et al. (1985) suggested that if the efficiency of acetate utilization depends on the availability of NADPH which is produced from the oxidation of glucogenic precursors, and that the administration of amino acids as casein may allow the synthesis of fat to proceed. If these precurors are limiting, however, acetate may be oxidized via substrate cycles, resulting in a lower efficiency of ME use. This hypothesis, however, has not been validated.

Ortigues et al. (1990) found that energetic efficiency increased

54% when the protein content of the diet was increased from approximately 9 to 12% by adding fishmeal to the diet of heifers fed a basal diet of straw and sugarbeet pulp. However when the two daily energy retentions of one heifer which were markedly negative were removed from the analysis, the efficiency of use of ME for energy gain of the first increment of fishmeal was not significantly different from either the basal diet or when the second increment of fishmeal was added.

In the present trial, and in those performed by Barry (1981) in lambs and Close et al. (1983) in pigs, protein intake did not affect energetic efficiency. Responses to protein supplementation, however, appear to be dependent on the physiological state of the animal (Ørskov, 1976) and on the balance of nutrients (Hartsook and Herschberger, 1971), hence effects of previous nutrition, age and total nutrient supply may well have an effect on the energetic response to protein supplementation and thus explain the variable results. A change in efficiency of ME utilization with dietary protein might be expected. Theoretical estimates of the conversion of dietary carbohydrate into fatty acids are approximately 82-85%, whereas the conversion of amino acids to protein ranges from 75-85% (Baldwin, 1980). However, results from feeding trails have indicated that the true efficiency of fat deposition is between 50 and 60% and that the efficiency of protein deposition may be as low as 10-15% (Old and Garrett, 1985). Although, estimates may vary, the efficiency of protein deposition does appear to be substantially lower than that for fat. Reeds and Fuller (1983) reviewed results which demonstrated that protein synthesis occurred at twice the rate of protein deposition thus it is likely that the low efficiency of protein deposition is a result of

the cost associated with protein turnover (Garrett and Johnson, 1983). Further, the rate of protein synthesis increases with increasing intake (Reeds and Fuller, 1983). Hence, it appears reasonable to expect that with higher protein diets, protein deposition is increased (Table 8; Close et al., 1983) and therefore energetic efficiency, per se, may be decreased.

The lambs used in the trial Walker and Norton (1971), in which protein supplementation essentially decreased efficiency of ME use, were 2-5 days old at the start of the 21 day trial. The animals used in the trials of Barry (1981), Close et al. (1983) and in the present trial, where energetic efficiency was not affected by protein supplementation, were weaned and essentially at different stage of growth than those used by Walker and Norton (1971) or MacRae et al. (1985). In contrast to the previous workers, the mature wethers used by MacRae et al. (1985) demonstrated an increase in energetic efficiency with casein infusions, hence the age of the animals may also affect the ability of the animal to respond to different protein intakes.

To summarize, no effect of protein on the efficiency of ME use was observed here. This may have been because the level of intake for the lambs was intermediate and it has been suggested that efficiencies of ME utilization are affected in opposite directions above and below maintenance (Walker and Norton, 1971; Blaxter and Boyne, 1978), because the animals were young, or because the positive effects of protein on energetic efficiency were negated by the increased proportion of energy retained as protein when higher protein diets were given. In light of these observations, and the limited and conflicting information on the

effects of diet on energetic efficiency, the conclusions drawn by Hennessy and Williamson (1990) and Leng (1989) of the effect of escape protein on energetic efficiency should be viewed with some caution. The conflicting results do, however, highlight the need for investigation of the interactive effects of age with diet, in respect to energetic efficiency.

2.4.7 Method for Measuring Energy Partitioning

Although, relatively, the effects of cold on heat production and energy retention in the lambs were consistent in the present trial whether measured by calorimetry or by the comparative slaughter procedure, the effects of diet and sex were inconsistent. These differences, however, may have been because differences between treatments were not significant due to the larger standard errors, particularly with the calorimetry technique.

The average 61% greater energy retention with the calorimetry procedure is in general agreement with observations from Waldo and Tyrell (1980), who found that energy retention estimated from calorimetry-balance studies was 30-50% greater than energy retention estimated from the comparative slaughter technique. Beever et al. (1988) noted that in comparing energy retention from the two techniques, the largest discrepancies were detected on the diets which promoted the lowest energy gains.

Geay (1984) proposed that, although differences between the two techniques may be significant, both techniques may describe the treatment effects correctly in relative values. Errors in calorimetry-balance measurements may, in part, be associated with irregular growth (Geay

1984). Geay (1984) also reported that differences observed in the two techniques are more dramatic in younger animals. In support of this, Graham (1982) suggested that responses in the energy expenditure of immature animals to changes in feed intake are slow. Hence, Graham (1982) proposed that some of the error evidenced in calorimetry trials may be a function of there being insufficient time for animals to adapt to their nutritional state. It is unlikely, however, that this lag time would be a significant contributor to the differences observed in this trial since animals remained on their originally assigned diet for the full duration of the 85 day trial.

The standard error for estimates of energy, protein and fat retention are much higher for the calorimetry trial than for the comparative slaughter measurements. For example, standard errors associated with calorimetry measurements were 2% of total heat production in the trial of Ortigues et al. (1990) in which more sheep were involved and 4% in that of Close et al. (1983). The standard errors for heat production in this trial were 4 to 5% of the total heat production measurements and thus were within an acceptable range. This large variation associated with calorimetric measurements is likely due to the accumulation of errors made when measuring inputs and outputs (Van Es 1980 cited by Geay, 1984). Close et al. (1983) was able to detect differences of 15 to 30% in heat production with different intakes with the calorimetry technique, hence calorimetry may be a useful tool when dealing with large treatment differences. It may not, however, be sensitive enough to detect more subtle changes such as the ones between diet in the present experiment.

Due to practical considerations, lambs were fed only once during calorimetry measurements as opposed to twice during the rest of the trial. A trend towards reduced heat production was observed by Rakes et al. (1961) in more frequently fed sheep, hence feeding once daily instead of twice daily could have increased the estimates of total heat production in the calorimetry trial. Therefore, differences between the two techniques may have been more exaggerated if measurements were made in sheep fed twice daily.

It is also possible that some of the inaccuracies lie with the comparative slaughter technique. For instance, in this experiment, the meat samples may not have been completely homogenous due the presence of the pieces of teeth and bone which could not be ground into small particles. In addition, the solvent used for fat extraction, petroleum ether, may result in an underestimate of fat concentration due the incomplete extraction of structural lipids (Nelson, 1975). However, the values obtained for fat and protein agree with the values for total energy retained, even though they were all measured separately, hence this could not have been a major source of error.

Although calorimetry measurements are often preferred to the more costly and destructive comparative slaughter measurements, for researchers concerned with absolute values the comparative slaughter technique appears to be much more accurate. This large standard error observed with calorimetry measurements may make it impossible to detect treatment differences whereas such differences may be detected with the comparative slaughter technique.

Table 2.1. Ingredients and composition of dietary dry matter

Item	Control	Canola	Fishmeal	SD[a]
Ingredients, % DM				
Barley straw	50	50	50	
Barley grain	30	30	30	
Rolled barley	17.2	5.6	12.6	
Canola meal		12.3		
Fishmeal, whitefish			6.1	
Molasses, beet	.26	.26	.26	
Salt[b]	.28	.28	.28	
Calcium Phosphate, 18% Ca; 21% P	.84	.33		
Limestone, 38% Ca	1.00	1.10	.55	
Vit. ADE[c]	.022	.022	.022	
Composition				
Gross energy, kcal/kg	4436	4656	4582	94.7
Acid detergent fibre, %	26.2	27.4	24.7	1.25
Neutral detergent fibre, %	47.9	48.8	44.2	2.17
Crude Protein, %	7.4	11.5	12.0	2.07
Ash, %	7.1	5.6	7.2	.77

[a]Standard deviation based on four samples per mean.
[b]Cobolt iodized salt contained 99% NaCl, .004% Co and .007% I.
[c]Vitamin premix contained 10,000,000 IU Vitamin A, 1,000,000 IU Vitamin D_3 and 10,000 IU Vitamin E per kilogram DM.

Table 2.2. The degradability of crude protein in straw and concentrates in situ[a]

Ingredient	A[b], %	B[c], %	k[d], %/hr	EDCP[e], %
Straw	46.9 ± 1.86	27.4 ± 11.08	1.3 ± 1.04	52.6
Barley	62.3 ± 2.07	30.8 ± 2.42	20.7 ± 4.35	87.1
Canola supplement	37.5 ± 2.81	67.6 ± 8.76	7.6 ± 2.23	78.3
Fishmeal supplement	41.9 ± 2.25	21.8 ± 2.68	19.1 ± 6.40	59.0

[a]Data are expressed as means ± SE. There are 6 observations per mean.
[b]Estimated soluble fraction.
[c]Estimated slowly degraded fraction.
[d]Estimated rate of degradation of the slowly degraded fraction.
[e]Estimated degradability of CP calculated at a rumen outflow rate of 5%/h.

Table 2.3. Least square means for daily intakes (per $kg^{.75}$) of dry matter (DM), gross energy (GE), organic matter (OM), nitrogen (N), acid detergent fibre (ADF), and neutral detergent fibre (NDF) in the digestibility trial

	n[a]	DM, g	GE, kcal	OM, g	N, g	ADF, g	NDF, g
Temperature							
Cold	34	75	345	70	1.31	20	36
Warm	36	71	322	66	1.23	18	33
SE[b]		.8	3.8	.8	.012	.2	.4
Probability[c]		<.01	<.01	<.01	<.01	<.01	<.01
Diet							
Control	24	74	329	68	.91[e]	19[e]	35[d]
Canola	22	73	342	70	1.43[d]	20[d]	36[d]
Fishmeal	24	72	329	66	1.46[d]	18[f]	32[e]
SE		1.0	4.7	.9	.015	.2	.4
Probability		.29	.09	.07	<.01	<.01	<.01
Sex							
Female	36	73	331	68	1.26	19	34
Male	34	73	336	68	1.27	19	34
SE		.8	3.8	.8	.012	.2	.4
Probability		.84	.33	.64	.68	.69	.51
Temperature * Diet							
Cold * Control	12	77	346	72	.96	20	37
Cold * Canola	10	77	356	72	1.48	21	38
Cold * Fishmeal	12	72	333	67	1.48	18	32
Warm * Control	12	70	312	64	.87	18	33
Warm * Canola	12	71	328	67	1.37	19	35
Warm * Fishmeal	12	71	326	66	1.44	17	31
SE		1.5	6.5	1.4	.021	.4	.6
Probability		.09	.10	.09	.17	.12	.09

[a]Number of observations within each treatment included two observations per animal.
[b]Standard error.
[c]Probability of observing a greater F-value
[d,e,f]Means within treatments with different superscripts are significantly different (P<.05).

Table 2.4. Least square means for the apparent digestibilities (%) for dry matter (DM), gross energy (GE), organic matter (OM), nitrogen (N), acid detergent fibre (ADF), and neutral detergent fibre (NDF)

	n[a]	DM	GE	OM	N	ADF	NDF
Temperature							
Cold	34	58.7	60.1	59.6	58.1	43.2	45.2
Warm	36	60.6	61.8	63.2	59.1	44.0	46.3
SE[b]		.49	.46	.71	.8	.79	.74
Probability[c]		.01	.02	.01	.37	.57	.42
Diet							
Control	24	59.0[e]	59.9[e]	60.0	47.7[e]	44.2[d]	46.1[e]
Canola	22	61.0[d]	62.3[d]	62.3	62.9[d]	46.8[d]	49.2[d]
Fishmeal	24	58.8[e]	60.7[de]	61.8	65.1[d]	39.8[e]	42.1[f]
SE		.60	.56	.88	.98	.94	.91
Probability		.04	.03	.20	<.01	<.01	<.01
Sex							
Female	36	60.2	61.3	62.3	58.2	44.6	46.8
Male	34	59.0	60.6	60.5	59.0	42.6	44.8
SE		.49	.46	.71	.8	.79	.74
Probability		.08	.30	.06	.45	.06	.05
Temperature * Diet							
Cold * Control	12	57.2	58.2	57.7	45.6	43.2	44.4
Cold * Canola	10	61.3	62.6	62.1	64.3	47.9	50.5
Cold * Fishmeal	12	57.5	59.6	59.0	64.3	38.6	40.8
Warm * Control	12	60.8	61.5	62.4	49.8	45.2	47.8
Warm * Canola	12	60.8	61.9	62.6	61.8	45.6	47.9
Warm * Fishmeal	12	60.1	61.9	64.6	65.8	41.1	43.3
SE		.85	.79	1.24	1.38	1.36	1.28
Probability		.07	.06	.15	.07	.21	.07

[a]Number of observations within each treatment included two observations per animal.
[b]Standard error.
[c]Probability of observing a greater F-value.
[d,e,f]Means within treatments with different superscripts are significantly different (P<.05).

Table 2.5. Least square means for initial and final weights, average daily gains (ADG) and gain to dry matter intake in the 85 day experiment

	n[a]	Initial wt,kg	Final[b] wt,kg	ADG[cd], g	Gain:DMI
Temperature					
Cold	17	21.8	28.8	85	.106
Warm	18	22.6	31.7	98	.125
SE[e]		.54	.64	4.6	.007
Probability[f]		.35	.01	.10	.061
Diet					
Control	12	21.3	28.6[h]	81	.104
Canola	11	22.5	30.5[gh]	91	.117
Fishmeal	12	22.8	31.5[g]	101	.120
SE		.66	.78	5.6	.009
Probability		.25	.04	.06	.221
Sex					
Female	18	21.3	27.9	87	.109
Male	17	23.1	32.5	96	.122
SE		.54	.4	4.6	.007
Probability		.03	<.01	.17	.199
Temperature * Diet					
Cold * Control	6	21.1	26.6	69	.102
Cold * Canola	5	21.9	29.3	88	.105
Cold * Fishmeal	6	22.6	30.9	96	.111
Warm * Control	6	21.6	30.4	95	.106
Warm * Canola	6	23.1	30.6	95	.130
Warm * Fishmeal	6	23.0	31.8	106	.140
SE		.93	1.11	7.9	.012
Probability		.89	.70	.40	.57

[a]Number of observations within each treatment.
[b]Covariate (dry matter intake) was significant for final weight (P<.002).
[c]Covariate (dry matter intake) was significant for ADG (P<.001).
[d]Average daily gain calculated over 85 days.
[e]Standard error.
[f]Probability of observing a greater F-value.
[g,h] Means within treatments with different superscripts are significantly different (P<.05).

Table 2.6. Least square means for daily nitrogen partitioning ($g/kg^{.75}$) and rumen ammonia and plasma urea nitrogen concentrations (mg/dl)

	n[a]	Intake	Urine	Feces[b]	Retention[c]	NH_3-N	Urea-N
Temperature							
Cold	34	1.31	.33	.51	.40	9.9	15.5
Warm	36	1.23	.27	.50	.52	9.8	14.4
SE[d]		.012	.016	.009	.031	.69	.51
Probability[e]		<.01	.05	.47	.04	.94	.24
Diet							
Control	24	.91[g]	.17[g]	.48[g]	.13[g]	4.6[h]	8.8[g]
Canola	22	1.43[f]	.35[f]	.52[f]	.57[f]	14.2[f]	17.1[f]
Fishmeal	24	1.46[f]	.40[f]	.52[f]	.68[f]	10.6[g]	18.9[f]
SE		.015	.02	.011	.038	.85	.63
Probability		<.01	<.01	.01	<.01	<.01	<.01
Sex							
Female	36	1.26	.30	.51	.45	9.6	14.4
Male	34	1.27	.31	.50	.47	10.0	15.4
SE		.01	.016	.009	.031	.69	.51
Probability		.68	.61	.27	.61	.71	.17
Temperature * Diet							
Cold * Control	12	.96	.17	.50	.14	5.5	8.5
Cold * Canola	10	1.48	.39	.50	.49	13.7	17.5
Cold * Fishmeal	12	1.48	.44	.53	.67	10.4	20.5
Warm * Control	12	.87	.16	.46	.23	3.8	9.1
Warm * Canola	12	1.37	.30	.54	.65	14.6	16.7
Warm * Fishmeal	12	1.44	.35	.50	.69	10.9	17.2
SE		.021	.028	.015	.054	.53	.88
Probability		.17	.23	.06	.23	.47	.14

[a]Number of observations within each treatment included two observations per animal.
[b]Covariate (dry matter intake) was significant for fecal nitrogen (P<.005).
[c]Covariate (dry matter intake) was significant for retained nitrogen (P<.002).
[d]Standard error.
[e]Probability of observing a greater F-value.
[f,g,h]Means within treatments with different superscripts are significantly different (P<.05).

Table 2.7. Least square means for daily methane and urine energy losses

	Methane				Urine			
	n[a]	kcal /kg$^{.75}$	%GE[b]	%DE[c]	n[d]	kcal /kg$^{.75}$	%GE	%DE
Temperature								
Cold	11	22.4	6.6	11.0	35	6.9	1.65	3.54
Warm	11	19.1	5.7	9.1	35	5.6	1.45	2.66
SE[e]		.93	.69	.46		.26	.081	.119
Probability[f]		.11	.12	.06		.01	<.01	<.01
Diet								
Control	7	20.8	6.2	10.6	24	4.7[h]	1.46[h]	2.45[h]
Canola	8	21.4	6.2	10.0	22	7.2[g]	2.12[g]	3.42[g]
Fishmeal	7	20.1	5.9	9.7	24	7.0[g]	2.08[g]	3.44[g]
SE		1.14	.33	.52		.32	.099	.242
Probability		.79	.81	.55		<.01	<.01	<.01
Sex								
Female	10	20.6	6.0	9.6	35	6.0	1.81	2.95
Male	12	20.9	6.2	10.6	35	6.6	1.97	3.25
SE		.93	.27	.46		.26	.081	.119
Probability		.88	.69	.17		.27	.17	.09
Temperature * Diet								
Cold * Control	3	23.9	7.1	12.1	5	5.0	1.62	2.80
Cold * Canola	4	23.2	6.7	11.0	6	8.2	2.45	3.95
Cold * Fishmeal	4	20.2	5.9	9.9	6	7.6	2.31	3.88
Warm * Control	4	17.6	5.4	9.0	6	4.5	1.31	2.10
Warm * Canola	4	19.5	5.7	8.9	6	6.1	1.79	2.88
Warm * Fishmeal	3	20.1	6.0	9.5	5	6.3	1.86	3.01
SE		1.61	.47	.73		.45	.14	.207
Probability		.31	.32	.32		.84	.46	.69

[a]Number of observations with measurements made twice on three animals per observation except in the case of female lambs fed the control diet in the cold and the fishmeal diet in the warm.
[b]Energy loss as a percentage of gross energy intake.
[c]Energy loss as a percentage of digestible energy intake.
[d]Number of observations within each treatment included two observations per animal.
[e]Standard error.
[f]Probability of observing a greater F-value.
[g,h]Means within treatments with different superscripts are significantly different (P<.05).

Table 2.8. Least square means for daily dry matter intake (DMI, g/kg$^{.75}$), metabolizable energy (ME) intake (kcal/kg$^{.75}$), heat production (kcal/kg$^{.75}$) and total retained energy, fat and protein (kcal/kg$^{.75}$) estimated from comparative slaughter and calorimetry techniques

	Comparative Slaughter[a]						Calorimetry[b]						
	n[c]	DMI	ME intake	Heat	Energy	Protein	Fat	n[d]	DMI	ME intake	Heat	Energy	Protein	Fat
Temperature														
Cold	17	83	194	173	22	6.6	16	11	77	177	146	32	17	24
Warm	18	78	213	186	30	8.5	22	11	71	186	130	53	17	27
SE[e]		1.0	2.5	2.9	1.0	.49	.9		1.6	2.9	5.5	6.9	1.1	6.2
Probability[f]		<.01	<.01	.02	<.01	.04	<.01		.04	.13	.28	.15	.91	.12
Diet														
Control	12	79	196[h]	172[h]	26	6.3	20	7	74	173	140	34	7[h]	27
Canola	11	81	210[g]	186[g]	26	8.1	18	8	75	190	148	45	21[g]	28
Fishmeal	12	80	204[gh]	181[gh]	27	8.2	19	7	73	182	130	49	23[g]	21
SE		1.2	3.1	3.5	1.2	.60	1.1		1.9	3.5	6.8	8.5	1.3	7.6
Probability		.64	.01	.04	.98	.06	.71		.67	.06	.66	.54	<.01	.97
Sex														
Female	18	81	201	178	26	7.3	19	10	74	188	138	52	17	38
Male	17	79	205	181	27	7.8	19	12	74	175	142	33	17	15
SE		1.0	2.5	2.9	1.0	.49	.9		1.6	2.9	5.5	6.9	1.1	6.2
Probability		.34	.27	.38	.54	.42	.94		.82	.02	.64	.12	.83	.09
Temperature * Diet														
Cold * Control	6	83	182	163	20	4.7	16	3	77	166	160	18	8	10
Cold * Canola	5	84	203	180	24	7.5	17	4	80	185	171	34	20	14
Cold * Fishmeal	6	81	197	177	22	7.8	15	4	75	179	140	43	23	20
Warm * Control	6	76	209	181	32	8.0	23	4	72	179	125	50	7	43
Warm * Canola	6	78	217	192	28	8.6	19	4	71	194	130	55	22	34
Warm * Fishmeal	6	78	212	185	30	8.7	22	3	70	186	122	54	23	32
SE		1.8	4.3	5.0	1.7	.85	1.6		2.7	5.0	9.5	12	1.9	10.8
Probability		.52	.20	.59	.07	.30	.25		.77	.86	.79	.76	.76	.69

[a]Covariate (dry matter intake) was significant for ME intake, heat production, and energy, fat and protein retention estimated from comparative slaughter (P<.05).

[b]Covariate (dry matter intake) was significant for ME intake and energy retention estimated from calorimetry measurements (P<.05).

[c]Number of animals within each treatment for the comparative slaughter measurements.

[d]Number of observations for the calorimetry trial with measurements made twice on three animals per observation except in the case of females fed the control diet in the cold and the fishmeal diet in the warm.

[e]Standard error.

[f]Probability of observing a greater F-value.

[g,h]Means within treatments with different superscripts are significantly different (P<.05).

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III GENERAL DISCUSSION

There are a number of reviews on the effects of cold on animal production (Young, 1981; Young et al., 1989) and on digestive responses to cold (Christopherson and Kennedy, 1983; Christopherson, 1989). The general effect of cold on production and digestibility outlined in the reviews were, in most cases, confirmed in the present trial. An exception was the effect of cold on methane production. Previous workers have found that methane losses decreased with cold temperatures, however, in this trial, losses tended to stay the same, or , when expressed as a percentage of DE intake, to increase. Although these results contrast with previous results, it is possible that methane production will only be reduced when the environmental temperature is below the lower critical temperature of the animal. Due to the fleece of the lambs in the trial, as well as the group housing for half of the 85 day trial, it is possible that the animals were not cold enough for methane production to be affected. Further, results from this trial as well as from others (Graham et al., 1959; Blaxter and Wainman, 1961; Rogerson, 1960) indicate that there may be a feeding level by temperature interaction with respect to methane production and that methane production may not be influenced by cold temperature at low feeding levels. This possible interaction, as well as the extent of cold-stress required to decrease methane production require further investigation.

The use of bypass protein is recommended by the NRC for ruminants, be they dairy (NRC, 1988), beef (NRC, 1984) or sheep (NRC, 1985), however a review of the literature reveals that responses of sheep and cattle to

escape protein are not consistent (eg. Klopfenstein et al., 1982; Coombe, 1985; Yilala and Bryant, 1985; Steen, 1985, 1988, 1989; Veira et al., 1988; Ortigues et al., 1990; Hennessy and Williamson, 1990; Hussein and Jordan, 1991; Petit et al., 1991; Brand et al., 1991). One of the problems associated with predicting responses to bypass protein supplementation is the large variety of basal diets used for these two species. Animal responses to escape protein supplementation have been more consistent with lower quality forages (Gill et al., 1987), however it is often difficult to know whether the observed responses may be have been as readily obtained with an RDP as well as with the UDP supplements. This trial was designed to distinguish between responses from these two types of supplements. The results obtained in this experiment support the theory (eg. Barry, 1981; Close et al., 1983) that increasing the protein intake of animals will result in an increased proportion of energy retained as protein. It has been suggested that increases in protein intake will improve the efficiency of ME utilization for growth (MacRae et al., 1985; Hennessy and Williamson, 1990), however, thus far, reports in the literature are inconclusive. No response in the efficiency of ME utilization was observed in the present trial with RDP or UDP supplementation.

Responses to bypass protein appear to be more consistent in tropical countries according to Leng (1989). Since a major difference between tropical and temperate climates is temperature, this experiment was designed to test for an interaction between bypass protein and environmental temperature. No such interaction was observed in this trial. Temperatures in Australia and Southeast Asia are often over 30°C

for long periods of time, hence the temperature used for the animals in the warm environment (22°C) may not have been high enough to elicit a response. Therefore a repetition of this trial with higher ambient temperatures for the warm treatment could provide some useful information. It is, however, difficult to accept suggestions that bypass protein will double production responses in Australia (Leng, personal comm.) solely through its action on energetic efficiency. Bypass protein has been shown to improve voluntary intake (eg. Gill et al., 1987; Brand et al., 1991), hence an improvement in production could be accomplished through such a response. In addition, microbial fermentation is limited with inadequate rumen NH_3-N levels, brought about by low levels of dietary protein (Satter and Slyter, 1974). Native grasses in Australia are relatively low in crude protein content, hence the observed responses may be a result of the protein supplementation as opposed to UDP supplementation.

Although bypass protein may by a useful tool in improving animal gains, some of these supplements, such as fishmeal, are expensive, hence caution must be used when recommending such a tool. There are less expensive supplements, however, it is advisable that the producer perform an analysis in which the potential benefits of escape protein be weighed against the cost of such a product.

In terms of cost, calorimetry measurements may be preferrable to the comparative slaughter technique for measurements of energy retention, however for absolute values, calorimetry measurements are not as accurate as those obtained from the comparative slaughter technique. Estimates from the calorimetry measurements tended to be 60% greater than those obtained from comparative slaughter measurements, which are similar to

differences measured by other workers (eg. Waldo and Tyrell, 1980). Further, standard errors tend to be much greater for the calorimetry measurements than the comparative slaughter measurements due to the errors associated with inputs and outputs (Van Es, 1980 cited by Geay, 1984). Therefore for estimates of energy retention, the comparative slaughter technique may be considered superior to calorimetry measurements.

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